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Studies on the Deep Sea Protobranchia; The Subfamily Spinulinae (Family Nuculanidae)

J. A. ALLEN AND H. L. SANDERS

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

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STUDIES ON THE DEEP SEA PROTOBRANCHIA; THE SUBFAMILY SPINULINAE (FAMILY NUCULANIDAE)

J. A. ALLEN[1]

H. L. SANDERS[2]

ABSTRACT. Species of the subgenera *Spinula* and *Bathyspinula* are combined within a new subfamily Spinulinae of the family Nuculanidae. Five species of the genus *Spinula* are described from the lower slope (500–2000 m) and abyss (2000–5000 m) of the Atlantic; four are new to the Atlantic, three are new to science, and one requires redescription. Detailed descriptions of their morphology are given and comparisons are made. It is suggested that the genus *Spinula* is a fast, subsurface burrower, capable of processing large amounts of sediment, and may be the abyssal counterpart of the shallow water Tellinacea. It is also suggested that, in association with the taking in of large quantities of sediment, these animals are modified to eject excessive amounts of pseudofaeces via the feeding aperture and with the aid of the posterior margin of the foot. This process may involve using the secretions of the 'byssal gland' as adhesive material to hold the flocculant waste together.

INTRODUCTION

In our first three papers in this series on the protobranchiate bivalves of the abyssal Atlantic (Sanders and Allen, 1973, 1977; Allen and Sanders, 1973) we investigated clearly defined groups which have characters that are in many ways extreme in form relative to the majority of the species of the Protobranchia. In the present paper we turn to the genus *Spinula*, which is represented by five species in our samples. These form a component part of a larger group of species exhibiting a spectrum of characters which we (as others before us) have found difficult to split into well-defined sub-units. All species of the group are characterized by having the shells rostrate posteriorly and at least a portion of the ligament internal. We place these together in a single family, the Nuculanidae, which we divide into three subfamilies: Spinulinae, Ledellinae, and Nuculaninae. The two latter subfamilies will be subjects of later papers in this series.

The proposed division is at variance with the conclusion of Filatova (1958) that *Spinula* is not related to the genus *Leda* (=*Nuculana*) as had been originally maintained by Dall (1908). Filatova (1958, 1976) referred *Spinula* to the family Malletiidae, stating that *Spinula*, in common with other members of this family, has an external ligament. She also noted anterior and posterior rows of fine hinge teeth separated by a toothless area below the umbo and an internal ligament.

Knudsen (1970) believed, as did Yonge (1939), that there is no justification for separating the Malletiidae from the Nuculanidae. For the present, we can state unequivocally that our own extensive material shows that Knudsen (1970) was correct in placing *Spinula* close to *Ledella* and *Nuculana* and that, while *Spinula* and *Ledella* are closely related (Table 1), *Spinula* and *Malletia* are clearly not.

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Family NUCULANIDAE Adams and Adams, 1858

Shell laterally compressed, oval in outline except for non-gaping rostrate posterior margin, shell frequently ornamented with concentric lines or ridges; ligament either entirely internal or with internal and external part; posterior siphons present, the inhalent and exhalent lumina of which may or may not be separated by fused tissue.

The three subfamilies may be separated on the form and position of the rostrum.

Subfamily Nuculaninae: rostrum formed as a continuous extension of dorsal shell margin; ventral margin of rostrum forms part of the convex ventral margin of the shell.

Subfamily Ledellinae: rostrum formed as a submedial beaked extension of the posterior shell margin; ventral concave flexure where the base of rostrum meets the convex ventral margin of shell (Table 1).

Subfamily Spinulinae: rostrum formed as a supramedial or occasionally medial extension of the posterior shell margin; ventral concave flexure where base of margin meets convex ventral margin of shell. A detailed diagnosis of this subfamily follows.

Subfamily SPINULINAE

Shell moderately robust, laterally compressed, oval in outline except for non-gaping rostrate posterior margin; rostrum triangulate, supramedial, rarely medial; shell glossy with concentric lines or ridges; ligament amphidetic with small internal triangular resilium and external outer layer extended by fused periostracum; hinge plate with small, chevron-shaped teeth; hind gut usually with numerous coils to right side of body or, exceptionally, a single loop to the right; palps moderately large with many narrow palp ridges; adductor muscles unequal in size, the anterior being larger; siphons formed by fusion of inner muscular mantle lobes ventral to incurrent siphon, no intersiphonal septum present.

Genus *Spinula* Dall, 1908

Type species: *Leda* (*Spinula*) *calcar* Dall, 1908, original designation.

The subfamily is monogeneric, *Spinula* being defined identically with the definition of the subfamily.

Two subgenera, *Spinula* and *Bathyspinula* Filatova, 1958 are recognized.

Subgenus *Spinula* Dall, 1908

Type species: as for genus.

Surface of shell with very fine concentric ridges; valves compact, relatively sturdy; periostracum smooth, glossy; tip of rostrum sharp.

Subgenus *Bathyspinula* Filatova, 1958

Type species: *Spinula* (*Bathyspinula*) *oceanica* Filatova, 1958, here designated.

In addition to concentric ridges on surface of shell, straight ridges in the form of striae obliquely intersect the concentric ridges; tip of rostrum blunt and rounded.

WORLD LIST OF *SPINULA* (NOT INCLUDING PRESENT RECORDS)

Spinula calcar (Dall, 1908). Recorded from the Pacific (4067–5535 m). See: Dall (1908); Hertlein and Strong (1940); Filatova (1958, 1976); Wolff (1960); Clarke (1962); Belyaev (1966); Knudsen (1970); Okutani (1974, 1975). *Spinula calcarella* (Dall, 1908) is now regarded as being identical to *S. calcar* (Knudsen, 1970; Filatova, 1976), although Filatova (1958) originally regarded it as a subspecies of *S. calcar* and not a *Bathyspinula*. We have not recorded this species in the Atlantic.

Spinula subexcisa (Dautzenberg and Fischer, 1897) (=*S. excisa* of authors, *non S. excisa* Philippi, 1844). Supposedly recorded throughout the following Basins (see p. 21): Labrador, N. America, Norway, W. Europe, Argentine, Agulhas, Angola, and the Mid-Atlantic Ridge in the region of the

Table 1. Comparison of subfamilies Ledellinae and Spinulinae.

Ledellinae	Spinulinae
1) Adductors equal in size or almost so.	1) Adductors unequal, posterior ⅓ size of anterior.
2) Posterior margin rostrate, medial or submedial.	2) Posterior margin rostrate, supramedial (rarely medial).
3) Ligament amphidetic, usually internal (except in *L. kermadecensis*); short central, inner and outer layers between hinge plates extended by fused periostracum.	3) Ligament amphidetic, with well-developed external part; internal part inset as resilium into hinge plate below umbo, externally extended by outer layer and fused periostracum.
4) Hind gut not spirally coiled to right (except in *L. crassa*, which is similar to *Spinula*).	4) Hind gut spirally coiled to right (except in *S. calcar*, which Knudsen [1970] figures with a single loop).
5) Shell robust, moderately inflated, usually with a matt surface; in some species, after reaching a given size, a change in spiral angle of growth produces a flattened shell margin.	5) Shell moderately robust, usually compressed, with glossy surface; no change in spiral angle of growth of shell.
6) Palps with (<30) palp ridges that are not exceptionally narrow.	6) Palps with numerous (<50) narrow palp ridges. Species of an equivalent size with 1½ to 2 times as many ridges as in *Ledella*.

Azores (1848–5153 m). See: Jeffreys (1876, 1879); Smith (1885); Clarke (1962).

Spinula pelvisshikokuensis Okutani, 1975. Recorded from the northwestern Pacific (3610 m). See: Okutani (1975).

Spinula filatovae Knudsen, 1967. Recorded from Gulf of Aden (2312 m). See: Knudsen (1967); Filatova (1976).

Spinula kermadecensis Knudsen, 1970. Recorded from Kermadec Trench (5850–5900 m). See: Knudsen (1970).

Spinula tasmanica Knudsen, 1970. Recorded from Tasman Sea (3580 m). See: Knudsen (1970); Filatova (1976).

Spinula sp. (Knudsen, 1970). Recorded from the Bay of Bengal (2820 m). See: Knudsen (1970).

Spinula (*Bathyspinula*) *bogorovi* Filatova, 1958. Recorded from the Riu Kiu Trench (6726 m). See: Filatova (1958); Wolff (1960); Clarke (1962); Belyaev (1966); Knudsen (1970); Filatova (1976).

Spinula (*Bathyspinula*) *oceanica* Filatova, 1958. Recorded from Japan Trench and northwestern Pacific (4653–6293 m). See: Filatova (1958, 1976); Wolff (1960); Suyehiro *et al.* (1962); Clarke (1962); Knudsen (1970); Okutani (1974).

Spinula (*Bathyspinula*) *vityazi* Filatova, 1964. Recorded from the Kurile-Kamchatka Trench (6435–9335 m). See: Filatova (1964, 1976); Wolff (1960) [*S.* (*B.*) *vitiazi—n. nudum*]; Suyehiro *et al.* (1962) (*S.* sp.); Clarke (1962) [*S.* (*B.*) *vityazi—n. nudum*]; Belyaev (1966); Knudsen (1970); Okutani (1974).

Spinula (*Bathyspinula*) *knudseni* Filatova, 1976. Recorded from the Kurile-Kamchatka Trench (6400–6800 m). See: Filatova (1976).

Spinula (*Bathyspinula*) *thorsoni* Filatova, 1976. Recorded from the Romanche Trench (6380–6430 m) and the Puerto Rico Trench (5220–6400 m). See: Filatova (1976).

SPECIES OF *SPINULA* FROM THE ATLANTIC

Spinula filatovae Knudsen, 1967
Figures 1–7 + 28

Spinula filatovae Knudsen, 1967: 257, fig. 8; Filatova, 1976: 219. (Type locality: JOHN MURRAY Expedition, Station 26, Gulf of Aden, Lat. 12°29′30″N, Long. 50°51′30″E; Holotype: BM(NH) 196640W.)

Previous records: Gulf of Aden, 2312 m (Knudsen, 1967). Western Indian Ocean, 3152–4340 m (Filatova, 1976).

Present records: Depth range = 1261–4340 m.

Specific Description. Knudsen (1967) described this species from one specimen taken from the Gulf of Aden; the soft parts were not studied in detail. The present specimens, all from the eastern Atlantic, are in sufficient number to confirm and extend Knudsen's description.

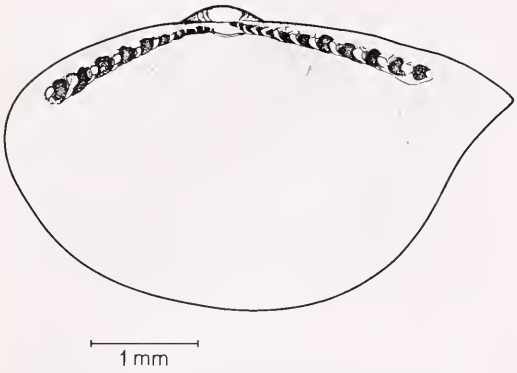

Figure 1. *Spinula filatovae*. Internal view of right valve of a specimen from Station S44 to show details of the hinge plate and shell outline.

Shell thin, with moderately strong concentric ridges, elongate-oval in outline with pointed posterior rostral extension; umbos somewhat anterior, low, beaks curved medially; dorsal margin weakly convex; antero-dorsal margin proximally straight and sloping downward to form smooth curve with anterior margin; postero-dorsal margin slightly convex, smoothly curved; rostrum short, sharply pointed, separated from ventral margin by slight sinuosity; ventral margin long, moderately convex, smoothly curved; anterior margin short, smoothly rounded; a ridge or keel, better developed distally, extends from umbo to point of rostral extension; postero-dorsally concentric ribs form right angles, the point of origin of which coincides with ridge; hinge plate long, rather narrow, anterior and posterior hinge plates with 10–12 chevron-shaped teeth, distal 5 in each series strong, proximal teeth progressively smaller, the innermost very reduced and difficult to discern; ligament amphidetic, internal part (resilium) small, approximately as long as wide, triangulate with truncated apex, outer layer externally extended anteriorly and posteriorly by fused periostracum to the level of the insertion of the sixth* tooth of both anterior and posterior hinge-tooth series (Fig. 1). Larval shell 385 μm in length; maximum recorded shell length 6.1 mm.

Our specimens correspond in most respects with *Spinula filatovae* as described by Knudsen (1967), but we would not regard the shell as thick when compared with species of the related genus *Ledella*. However, this is a subjective term, and there is no doubt that for an

* Numbered from the distal ends of the series.

TABLE 2. RECORDS FOR *Spinula filatovae* KNUDSEN.

Cruise	No.	Station no.	Depth (m)	No. of specimens	Latitude	Longitude	Gear	Date
				West Europe Basin				
SARSIA	—	S.44	1739	43	43°40.8′N	3°35.2′W	ES*	16.7.69
SARSIA	—	7610	1100–1185	12	43°42.5′N	3°48.6′W	Agassiz Dredge	10.9.76
				Cape Verde Basin				
ATLANTIS II	31	142	1624–1796	19	10°30.0′N	17°51.5′W	ES	5.2.67
				Guinea Basin				
WALDA	—	DS27	1261	1	3°30.7′N	5°31.8′E	ES	30.8.71
WALDA	—	DS28	1376	49	4°21.2′N	4°35.2′E	ES	30.8.71

* Epibenthic sled.

abyssal species this has a well-calcified shell. The figure of the type (Knudsen, 1967), admirably drawn by the late Paul Winther, is entirely accurate. Only *S. tasmanica* approaches the present species in general shape (Knudsen, 1970), but it differs in being stouter, having a heavy hinge plate with massive teeth, and having a more prominent posterior rostrum.

The amphidetic ligament consists of a small, triangular wedge-shaped internal part, the resilium, and an external part extending anterior and posterior to the umbo. The dorsal surface of the resilium is visible externally and consists of an inner layer overlain dorsally and distally and to some extent laterally by the outer layer. Dorsally, the resilium is overlain by a thin layer of fused periostracum. The external ligament is arched, elongate, and spindle-shaped in outline. It is connected anteriorly and posteriorly to the internal ligament by a very narrow neck of material. The external extensions of the ligament comprise an outer layer and thickened fused periostracum, the latter extending beyond the limits of the outer layer.

Morphology. With the exception of the posterior margin, the structure of the mantle is little modified. The mantle edge is for the most part not fused. Posteriorly, a combined inhalent and exhalent siphon is present, formed by fusion of inner muscular mantle lobe. A specialized area below the siphon almost certainly marks the point at which the palp proboscides are extended onto the sediment. A single siphonal tentacle is present on the left or right side, and on the anteroventral mantle margin there is a pair of anterior sense organs. Both of these structures are specializations of the middle sensory mantle lobe (see p. 24).

The siphons, combined as a somewhat laterally compressed tube, possess internally and laterally a series of ridges, of which one pair (left and right midlateral) originates from the posterior ends of the gill axes. Within the ridges, between inner and outer epithelium, a regular series of fine longitudinal muscle strands lie parallel to and equally spaced from each other (Figs. 2, 19). There is little or no hemocoelic space within the siphon. It is doubtful if the low-crested lateral ridges permanently separate an inhalent from an exhalent part by their approximation. No interlocking cilia can be seen in section. Scattered mucous cells are present in the inner epithelium. The anus lies immediately dorsal to the inner limit of the siphon, above the origin of the axial ridges, so that faeces tend to be extruded into the dorsal half of the siphonal tube. The ridges almost certainly act as guides for the passage of the faeces. The diameter of the faecal rod is about half the height of the lumen of the siphon, and fragments of the faecal rod have been observed dorsally. The gills act as a pump; thus on the upstroke faeces may be extruded as water is passing anteriorly along the lower half of the lumen due to the reduced pressure within the lower part of the mantle cavity. As in all protobranchs, the faecal rod is solid and does not easily fragment. Alternatively, water could pass into the mantle via the feeding aperture ventral to the siphons, although this is unlikely if the animal is buried to the extent its morphology suggests (see p. 28). The siphons can be completely retracted within the shell and are extended from a position immediately ventral to the posterior rostral extension of the shell. In the retracted state, the siphons are bent into an S-shape. Three retractor muscles extend into the mantle tissue at the posterior limit of the siphonal embayment.

Ventral to the siphons is a broad and deep specialized area of the mantle that is undoubtedly associated with feeding and which we refer to as the feeding aperture (Sanders and Allen, 1977) (Fig. 2). Here, the inner mantle lobe is enlarged both in thickness and width and much folded in the contracted state. Immediately *internal* to the muscular lobe is an

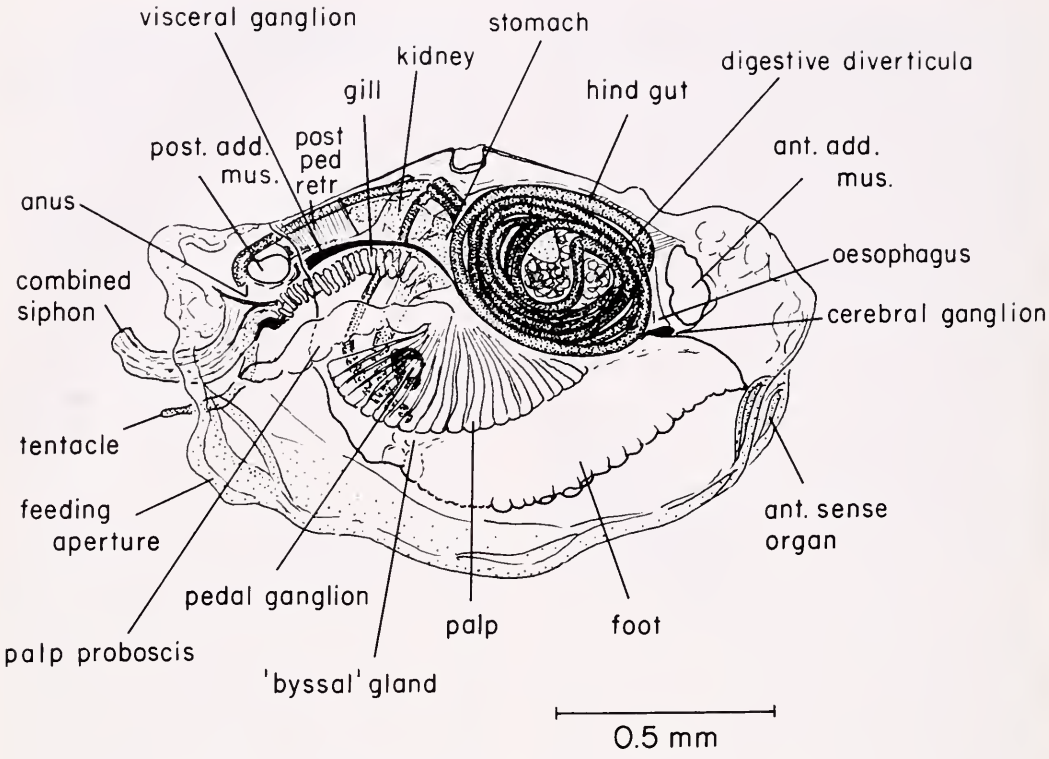

Figure 2. *Spinula filatovae.* Semidiagrammatic view of right side of the animal to show disposition of the organs.

additional lobe that is thinner and narrower than the former, but which lies parallel to it and extends the length of the feeding aperture. The epithelium on the ventral side of the additional lobe, the dorsal side of the muscular lobe, and the epithelium between the two, is richly supplied with acidophilic gland cells. This band of gland cells is continued anteriorly to the inside of the inner muscular lobe, although the cells here are fewer in number. Internal to the feeding aperture, there is a series of fine radiating pallial retractor muscles, and it is clear that this area of the mantle is capable of considerable extension. The tips of the contracted palp proboscides lie close to the second mantle lobe. Although there is no fusion ventrally to form a separate aperture, the opposing inner muscular lobes undoubtedly come together at this point and thus separate the feeding aperture from the extensive pedal gape.

The adductor muscles are unequal in size (Fig. 2), with the 'quick' and 'catch' parts obvious (Fig. 4). The smaller posterior adductor muscle is pear-shaped in outline. The anterior adductor is crescent-shaped and about 2.5 times as large in cross section as the posterior. Immediately below the anterior adductor, at the mantle edge, is the anterior sense organ (see p. 24). A single siphonal tentacle, common to many protobranch bivalves, arises from a short pocket on either the right or left side of the base of the siphon. The tentacle is developed from the middle sensory lobe of the mantle. It consists of an elongate, finely tapering cone which in transverse section

comprises a single outer layer of large cuboid epithelial cells which appear finely granular and may be secretory (Fig. 26a). To the inside is a single layer of elongate connective-tissue cells between which are scattered gland cells with ducts to the outside. In the central core is a large nerve together with a few fine muscle cells. As in the case of the siphon, although there is some haemocoelic space, it is not large. The tentacle clearly has a sensory function, but it may also assist in the cleansing of the siphonal region, including the feeding aperture.

The gills lie parallel to the dorsal posterior shell margin (Fig. 2). They are well developed with approximately 26 gill plates to each side of the axis. The outer and inner demibranchs are attached to the mantle and body, respectively, by tissue juctions. Posterior to the foot, the last three or four plates of the opposing inner demibranchs join. The gill axes join with the siphonal ridges.

The palps are moderately large and, depending on the size of the animal, have approximately 25–50 closely spaced ridges on their inner faces. The palp proboscides are relatively slender. The palps extend across the posterior quarter of the body. The mouth is set behind, but close to, the anterior adductor muscle.

The foot is extremely well developed and of typical nuculanid form, having a narrow base (Fig. 3). The divided sole is elongate and has finely papillate edges. Due to the presence internally of a large 'byssal' gland, the posterior ventral margin of the foot bulges laterally. A highly muscular foot must indicate active locomotion.

The posterior pedal retractor muscles comprise a thick, wide strap that inserts onto the shell on either side of the hind gut anterior to the posterior adductor muscle (Fig. 2). There is also a small postero-lateral muscle lying immediately posterior to the stomach (Fig. 4). Three major pairs of anterior pedal retractor muscles arise anteriorly from the base of

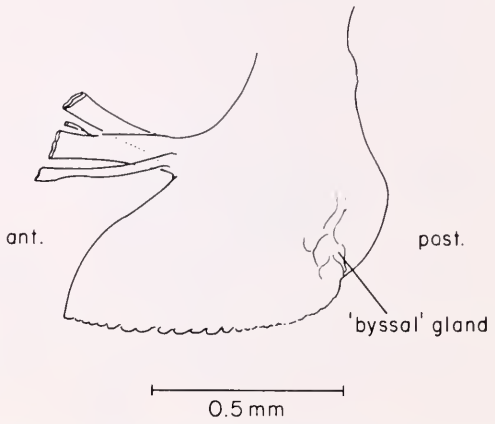

Figure 3. *Spinula filatovae*. Lateral view of the foot to show position of the left series of anterior pedal retractor muscles.

the foot and insert posterior to the anterior adductor on either side of the oesophagus (Fig. 4a). These overlap one another where they join the foot: the innermost muscle having the most posterior insertion on the shell; the outermost, the most anterior insertion. In section, the innermost muscle is seen to be split in the sagittal plane.

The cerebral ganglia are relatively small while the visceral are elongate. The pedal ganglia, which are the largest, lie far posterior within the foot close to the mid gut and are relatively ventral in position in comparison with other protobranch bivalves (Fig. 2). A large statocyst is associated with each pedal ganglion and lies dorsal to it.

The mouth is displaced posteriorly to a small extent; it opens to a relatively long oesophagus that curves anteriorly to the posterior face of the anterior adductor before passing posteriorly to the stomach. The oesophagus widens considerably just before joining the stomach (Fig. 4a). The stomach and style sac lie diagonally within the body.

The stomach and style sac are huge, taking up most of the central body space. The stomach externally is dark brown in

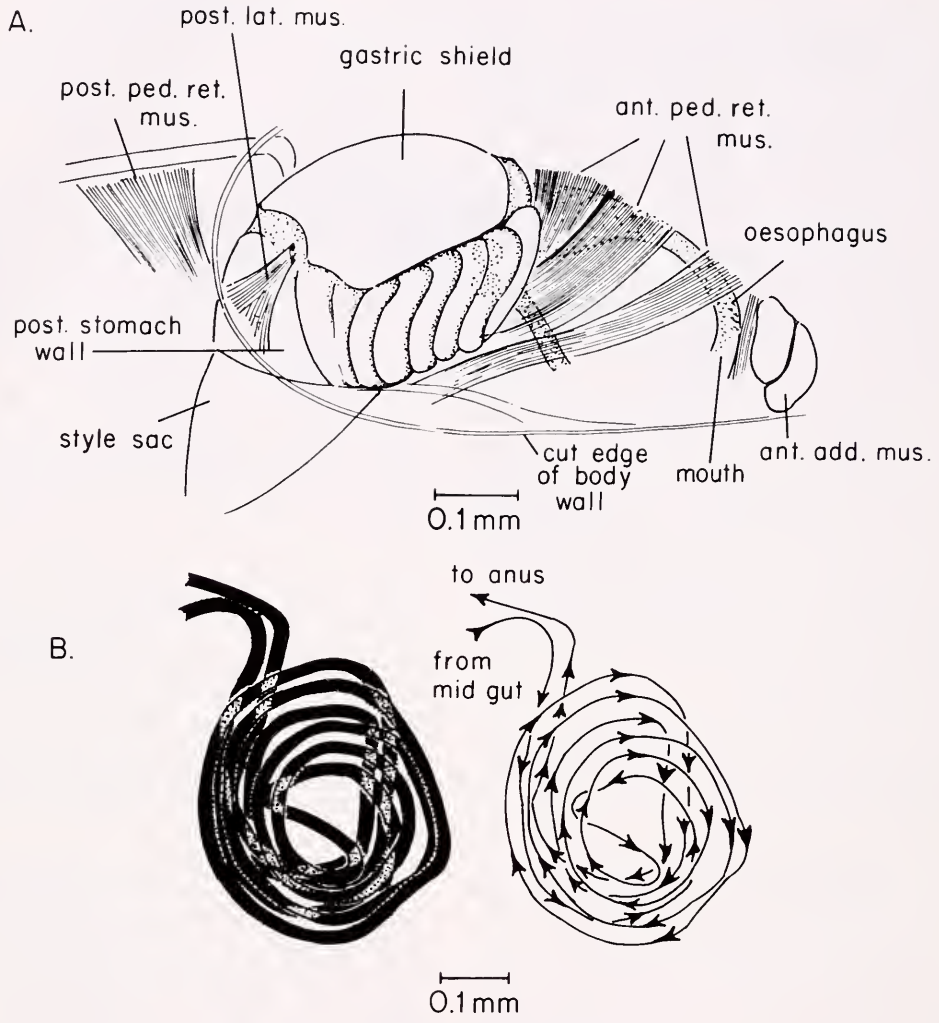

Figure 4. *Spinula filatovae*. A. Detail of the external features of the right side of the stomach and associated pedal muscles. B. Detail of the disposition of the hind gut coils viewed from the right side.

color. There is a large gastric shield that occupies more than one-third of the stomach wall. It is antero-dorsal in position and extends laterally, but more extensively to the left than to the right (Fig. 5). The remaining anterior wall is occupied by eight broad ciliated ridges (Fig. 4a), and at their anterior limit there are the apertures of three ducts leading to the digestive diverticula. The posterior wall of the stomach adjacent to the style sac appears to be without ridges. The stomach is cradled by the anterior, posterior, and postero-lateral pedal retractor muscles which must, on contraction, exert a considerable pressure on the stomach and constitute a major force pushing material through the gut. It is probably significant that the digestive ducts are far anterior and thus are anterior to the main

muscular force. As a result, material will not be squeezed into the digestive gland. Although the hind gut is ciliated and without obvious musculature, it is doubtful whether the cilia can be the main motive force moving material in the long hind gut. There is little or no space between faecal rod and gut wall.

From a position dorsal to the pedal ganglia, the hind gut passes posterior to the ganglia deep into the foot and curves antero-ventrally to the ganglia. It then retraces a course parallel to the descending section before passing to the right side of the body at a point immediately below the internal ligament. On the right side, the hind gut forms six tightly packed coils (Fig. 4b) before passing mid-dorsally over the posterior adductor muscle to the anus. There is no penetration by the body tissue of the blood space of the right mantle such as is seen in the Tindariidae (Sanders and Allen, 1977). There is no typhlosole present in the hind gut.

Material in the gut consists of fine clay particles and various skeletal remains that are too finely fragmented to identify except to note that many are pieces of diatom frustules belonging to many species. Material in the stomach looks little different from that in the hind gut. Little or no material is present in the lumen of the digestive tubules, and no skeletal remains were noted in the tubule cells.

The digestive gland is present both to the right and left of the body and, for the most part, lies anterior to the stomach. On the right side it is surrounded by the coils of the gut (Figs. 2, 5). There are three primary ducts leading from the digestive gland, two on the left side of the stomach below the base of the exceptionally large tooth on the gastric shield and a third, slightly more anterior, on the right ventral wall of the stomach (Fig. 5).

The digestive gland cells are similar to those seen in other protobranch bivalves. Interstitial cells are scattered at the periphery of the tubules, and some of these,

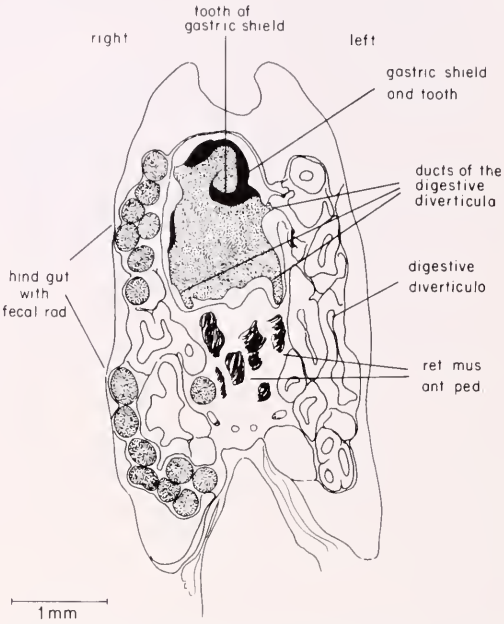

Figure 5. *Spinula filatovae*. Transverse section through viscera to show stomach and hind gut coils.

like the epithelial cells of the digestive ducts, contain highly refractile golden granules in the cytoplasm. In section, the vacuolated cells appear to be actively cutting off spherules into the lumen of the tubule. In addition, at the base of many of the vacuolated cells, there are clear spherical inclusions which may be the contents of vacuoles. From the apparent lack of food material in the tubule cells, it seems almost certain that much, if not all, digestion is extracellular. The kidney is moderately large and, as a feature common to many deep-sea bivalves (Allen and Turner, 1974; Oliver and Allen, personal observation), extends forward on either side of the posterior half of the stomach. A single layer of cuboid epithelial cells lines the wall of the kidney. The lumina of the left and right sides cross-connect below the hind gut posterior to the point where the hind gut passes through the ventricle of the heart.

Reproduction. Sexes are separate; go-

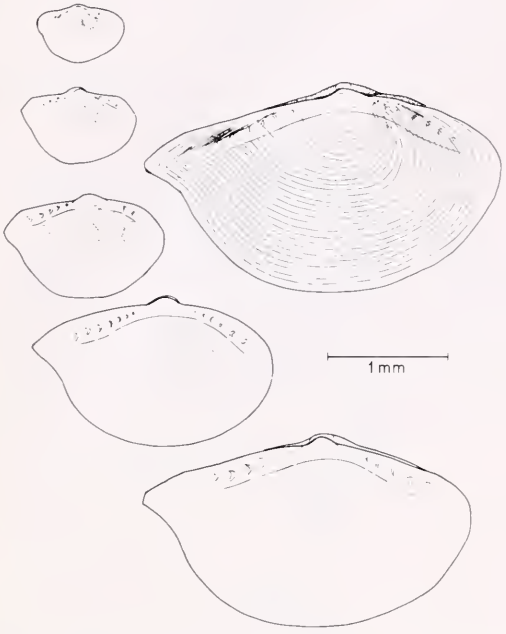

Figure 6. *Spinula filatovae*. Lateral views of a series of specimens to show change in shell outline with increasing size.

nads were only observed in a few specimens of 2.6 mm total length and above. Egg numbers are small, about 20 in a specimen of 2.6 mm. Several of the larger specimens (3.9 mm) appear to be spent. The gonads overlie the lateral and dorsal side of the viscera and are in a similar position on each side of the body. Because of lack of maturity, maximum egg diameter could not be determined. At maximum the gonad forms a ring around the coils of the hind gut or, on the left, the digestive diverticula. For the most part, the larger the animal the more mature is the gonad; however, not all large specimens have maturing gonads. The gonadal aperture lies close to the apertures of the kidney, anterior to the posterior pedal retractor muscles.

Growth. The larval shell is large (approx. 385 μm in length). The adult shell and rostrum become relatively more elongate with growth. Height to total length ratios and posterior length (=distance from umbo to distal margin) to total length ratios confirm the visual observation (Figs. 6, 7). The minimum length recorded is 1.2 mm, the maximum 6.1 mm. Both of the largest samples (D.S. 28 and S. 44) from the Canaries and Biscay respectively have similar length frequency histogram to size range (Fig. 7). There are no clear peaks to be seen, suggesting perhaps that the production is not confined to a short breeding season.

Spinula sp.
Figures 8–10 + 28

Records: Depth range = 4800–5000 m.

Because two of the three specimens have been lost and the third has been decalcified and made into a slide for the study of its soft-part anatomy, this species will not be named.

Description. Shell stout, thick, with strong, even, concentric ridges, somewhat elongate-oval in outline, rostrum short, bluntly pointed; umbos raised, moderately prominent, inflated, slightly posterior of middle, beaks medially curved; dorsal margin strongly convex; longer antero-dorsal margin slopes sharply downward to form smooth curve with anterior margin; shorter postero-dorsal margin almost straight to about level of distal end of posterior hinge plate, thereafter angled ventrally to form short, blunt rostrum separated from ventral margin by slight sinuosity; ventral margin long, moderately convex, smoothly curved; weak, although wide, keel extends from umbonal region to limit of rostrum; concentric ridges turn sharply at right angles where they cross the keel; hinge plate broad, strong, relatively long; anterior and posterior hinge plates with about 10 chevron-shaped teeth, distal 5 large and strong, more proximal teeth progressively smaller, most medial teeth so reduced as to be difficult to see; ligament amphidetic, internal part (resilium) large and

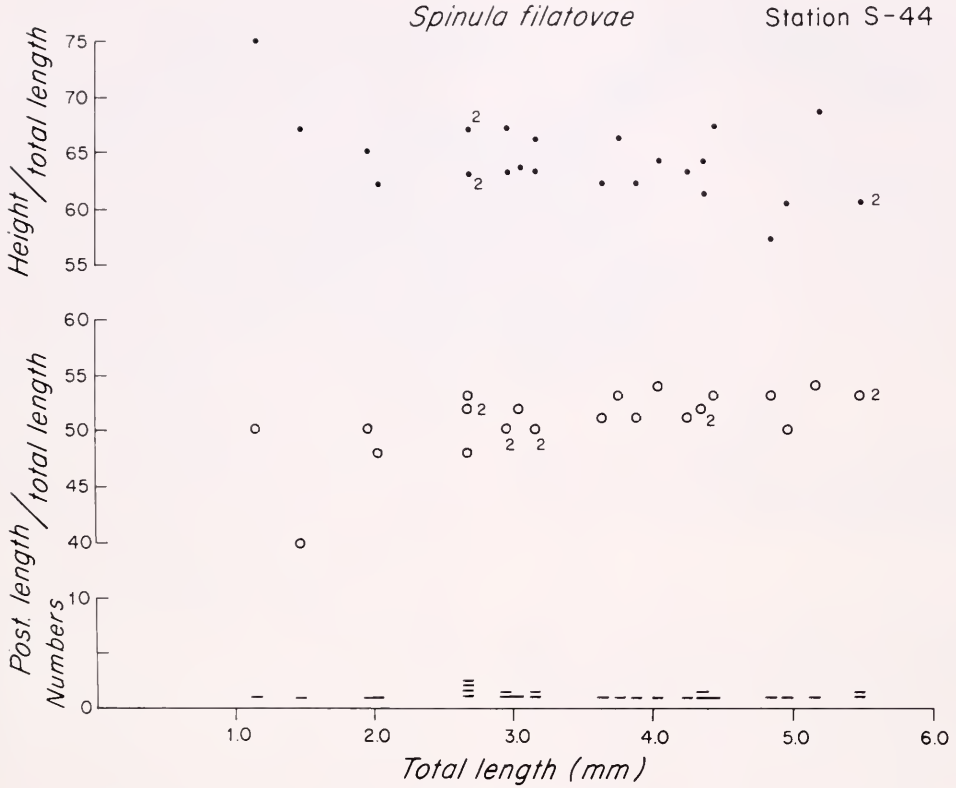

Figure 7. *Spinula filatovae.* Changing shell shape with increasing size as measured by the ratios height/total length and posterior shell length (umbo-rostrum)/total length to total length.

triangulate, with external extension elongate, narrow, anterior and posterior parts of approximately equal length, extending to level of fifth tooth, both on anterior and posterior hinge plate. Maximum recorded shell length 3.8 mm.

Of other described species of *Spinula*, only *S. tasmanica* has such a thick hinge plate and large teeth (Fig. 8); however, *S. tasmanica* is more elongate with a sharply pointed rostrum and with a low umbo clearly anterior in position (Knudsen, 1970).

Morphology. As we have only three specimens of this species, sections were not taken, and the following description is from a single specimen as a whole mount stained in hematoxylin (MCZ 279903).

The mantle structures differ little from those described for *Spinula filatovae.* The combined siphon is particularly large and deep. The feeding aperture is extensive, and the inner mantle lobe is extremely deep. It should be noted that the ventral posterior corner of the foot is extended and lies close to the feeding aperture and may well aid in pushing out the pseudofaeces from the mantle cavity, as happens in other protobranch bivalves.

The anterior sense organ is far anterior, in advance of the anterior limit of the anterior adductor muscle.

The adductor muscles are markedly unequal in size. The posterior muscle is oval, the long axis parallel to the dorsal margin of the shell. The anterior adduc-

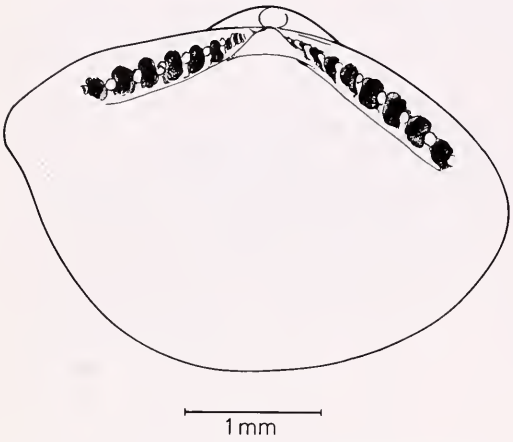

Figure 8. Unnamed species of *Spinula*. Internal view of left valve of a specimen from Station 83 to show details of hinge plates and shell outline.

tor muscle is more rounded, the larger 'quick' and smaller 'catch' parts being clearly visible. The siphonal tentacle originates on the right side and is inserted close to the base of the siphon.

The foot, while large, is not as large as it is in the other species described here. However, the 'byssal' gland is extremely large and spherical in form.

The gills are carried high in the mantle cavity parallel to the postero-dorsal shell margin. Thirteen gill plates are present on each demibranch in the present specimen. The mouth is set just posterior to the anterior adductor, the palps extending little more than half way across the body. In this specimen there are 30 fine ridges; the anterior part of the right palps is overlain by the coils of the hind gut. The contracted palp proboscides are noticeably short and stubby.

The stomach and style sac are relatively small, barely extending into the ventral half of the foot. Similarly, the hind gut does not extend deep into the foot, as is the case in *Spinula filatova*. Like the latter species, the first section of the hind gut lies close to the posterior body wall and extends just ventral to the pedal ganglion, where it turns dorsally taking one V-turn behind the stomach before passing to the right side of the body at a point close to the posterior dorsal margin of the shell. It forms seven visible coils on the right hand side of the body which are stacked one above the other; each coil is offset in an anterior direction adjacent to the anterior inner hinge margin.

The pedal ganglion is large, positioned in the posterior part of the neck of the foot. The visceral ganglion is cylindrical, terminating close to the posterior adductor muscle. The visceral-cerebral commissure parallels the gill axis and the ventral margin of the coils of the hind gut. Unfortunately, the specimen is a maturing male, so the cerebral ganglion and part of the hind gut are obscured by the testis.

Spinula hilleri new species
Figures 11–15 + 28

Holotype: MCZ 279904. (Type locality: ATLANTIS II, Cruise 42, Station 195, Angola Basin, Lat. 14°49.0'S, Long. 9°56.0'W, in 3797 m.)

Records: Throughout the Atlantic. Depth range = 2044–5227 m.

Specific Description. Shell moderately strong and slender, ornamented with

Table 3. Records for *Spinula* sp.

Cruise	No.	Station no.	Depth (m)	No. of specimens	Latitude	Longitude	Gear	Date
North America Basin								
ATLANTIS II	24	121	4800	1	35°50.0'N	65°11.0'W	ES	21.8.66
ATLANTIS II	24	123	4853	1	37°29.0'N	64°14.0'W	ES	22.8.66
CHAIN	50	83	5000	1	34°46.5'N	66°30.0'W	ES	3.7.65

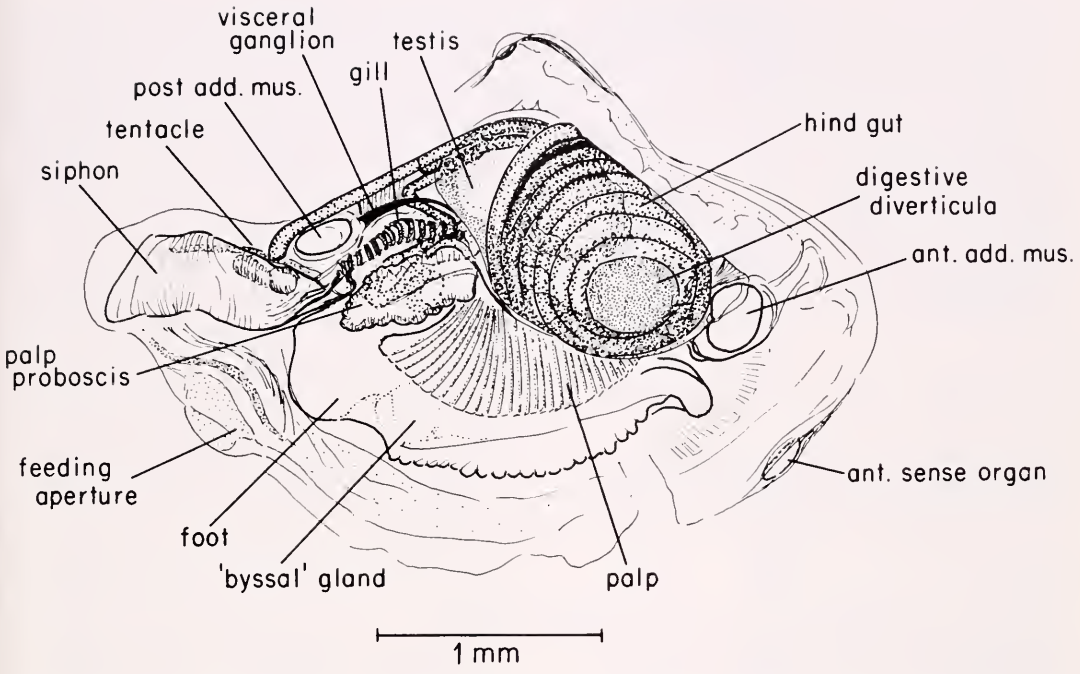

Figure 9. Unnamed species of *Spinula*. Semidiagrammatic view of right side of the animal to show disposition of the organs.

even concentric ridges; rostrum short, sharply pointed; umbos slightly anterior in position, in larger specimens small with low profile, beaks medially curve; dorsal margin moderately convex; antero-dorsal margin sloping sharply to form smooth curve with anterior margin; postero-dorsal margin nearly straight between umbo and distal edge of hinge plate, thereafter angling abruptly to form a short, usually sharp, pointed rostrum demarked from ventral margin by a concave sinuosity; ventral margin long, smoothly curved, convex, with greatest convexity in larger shells adjacent to posterior sinus (i.e., maximum shell height posterior to umbo); keel present, extending from umbo to point of rostrum, weakly developed near rostrum, becoming strong anteriorly where concentric lines form a sharp angle; hinge broad, strong and relatively long; anterior hinge plate

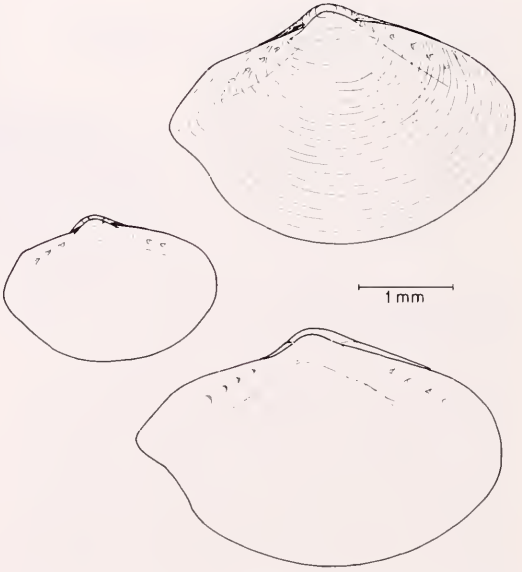

Figure 10. Unnamed species of *Spinula*. Lateral views of the three specimens recorded from our samples, to show variation in the shell outline.

TABLE 4. RECORDS FOR *Spinula hilleri* NEW SPECIES.

Cruise	No.	Station no.	Depth (m)	No. of specimens	Latitude	Longitude	Gear	Date
				Angola Basin				
ATLANTIS II	42	195	3797	98	14°49.0′–14°40.0′S	9°56.0′–9°54.0′E	ES	19.5.68
ATLANTIS II	42	196	4612–4630	2	10°29.0′S	9°03.0′–9°04.0′E	ES	21.5.68
ATLANTIS II	42	197	4592–4597	9	10°29.0′S	9°40.0′E	ES	21.5.68
ATLANTIS II	42	198	4559–4566	3	10°24.0′S	9°09.0′E	ES	21.5.68
WALDA		CY13	2044	3	12°03.7′S	12°22.3′E	T*	10.7.71
				Cape Verde Basin				
ATLANTIS II	31	145	2842–2891	1	10°39.5′N	17°44.5′W	ES	6.2.67
				Canary Basin				
DISCOVERY		6710	2670	1	27°23.6′N	15°39.6′W	ES	19.3.68
DISCOVERY		6711	2988	1	27°14.9′N	15°36.3′W	ES	19.3.68
				Sierra Leone Basin				
WALDA		CY21	3034	1	0°40.1′S	6°48.8′E	T	1.8.71
WALDA		CY23	2231	2	0°45.1′N	8°27.2′E	T	2.8.71
				West Europe Basin				
CHAIN	106	323	3350	1	50°08.3′N	13°53.7′W	ES	21.8.72
POLYGAS		DS15	2264	1	47°35.2′N	8°46.1′W	ES	23.10.72
				Brazil Basin				
ATLANTIS II	31	155	3730–3783	4	0°03.0′S	27°48.0′W	ES	13.2.67
ATLANTIS II	31	156	3459	8	0°46.0′–0°46.5′S	29°28.0′–29°24.0′W	ES	14.2.67
				Argentine Basin				
ATLANTIS II	60	242	4382–4405	5	38°16.9′S	51°56.1′W	ES	13.3.71
ATLANTIS II	60	247	5209–5227	24	43°33.0′S	48°58.0′W	ES	17.3.71
				Guiana Basin				
KNORR	25	303	2842–2853	4	8°28.8′N	56°04.5′W	ES	1.3.72
KNORR	25	306	3392–3429	5	9°31.1′N	56°20.6′W	ES	2.3.72

* Trawl.

with about 13 chevron-shaped teeth, posterior hinge plate with about 11 teeth (number depending on size of animal); distal teeth strong and well developed, proximal teeth progressively smaller, with those bordering the internal ligament minute and rudimentary; ligament amphidetic, internal part (resilium) triangulate, external extensions elongate, equal in length, and extending to level of fifth or sixth tooth. Maximum recorded shell length 8.7 mm.

We name this species after Captain Emerson Hiller of the Woods Hole Oceanographic Institution, whose superb seamanship has enabled us to trawl successfully at greath depths and with great precision throughout the Atlantic Ocean.

Morphology. Spinula hilleri has essentially the same morphology as the other species described here (Fig. 12). Mantle structures differ only in that the combined siphon appears to be very large, even in the contracted state, and that the anterior sense organ lies far anterior. The adductor muscles are relatively small and

unequal in size, the anterior being 2 to 3 times the size of the posterior.

The gills are moderately small, each with approximately 21 plates to each demibranch. The palps are large, with as many as 33 fine ridges; the number, as in the case of the gill plates, is dependent on the size of the individual.

The foot, although slender, is very large in this species, with a more anteriorly directed attitude than in *S. filatovae* and the unnamed species. There is a considerable number of fringing papillae which are somewhat larger than in the other species. The form of the foot suggests that this is an active, fast moving species. In fact, it is probably no coincidence that in this species the adductor muscles are relatively small, there possibly being no prolonged closure of the shell. In contrast, the pedal retractor muscles are well developed and may well assist in the adduction of the valves when the foot is fully contracted (Allen and Sanders, 1969). Probably also associated with increased activity is the large size of the ganglia, in particular the pedal. The heel of the foot is extended pos-

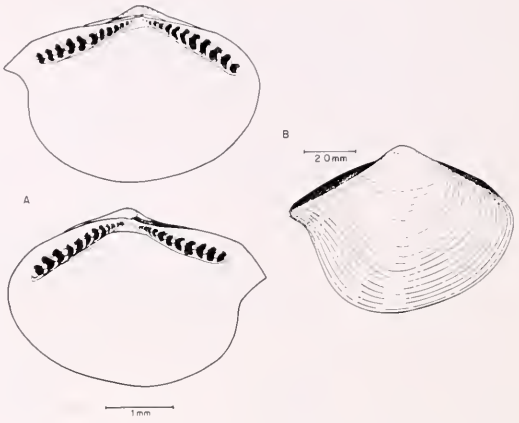

Figure 11. *Spinula hilleri.* A. Internal views of right and left valves of a specimen from Station 155 to show details of hinge plates and shell outline. B. Lateral view of right valve of holotype (MCZ 279904) from Station 195.

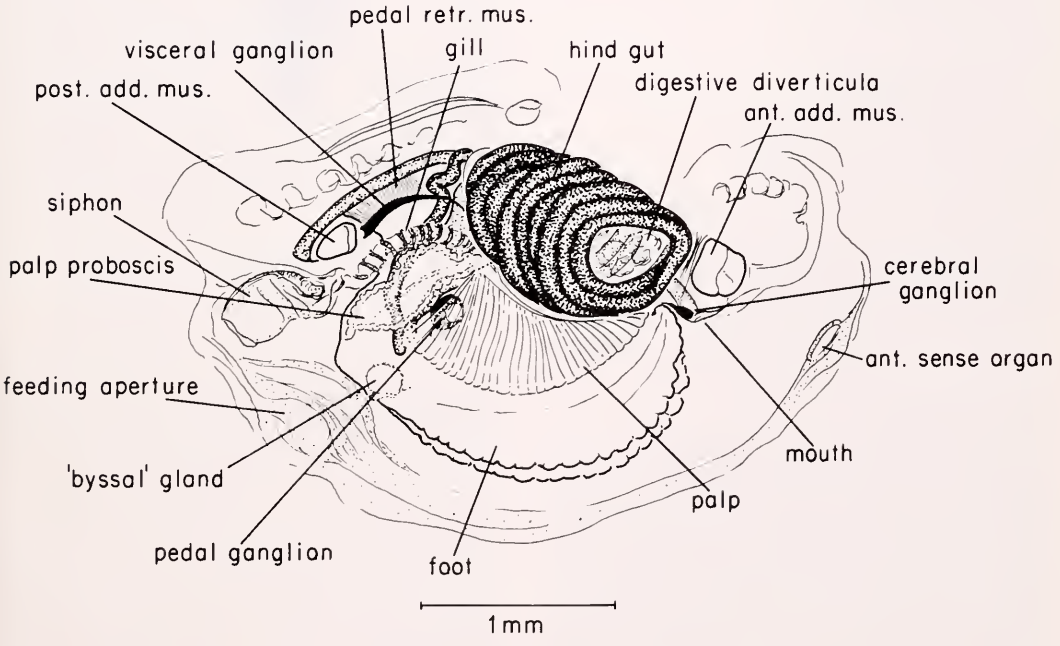

Figure 12. *Spinula hilleri.* Semidiagrammatic view of right side of the animal to show disposition of the organs.

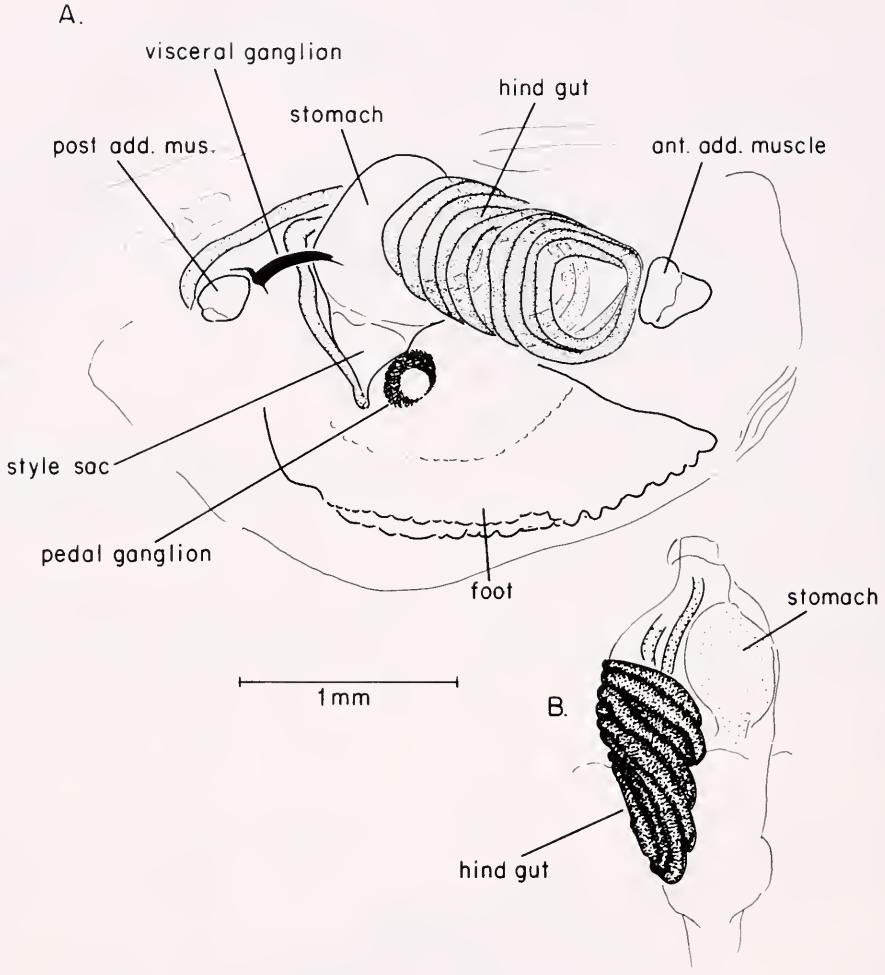

Figure 13. *Spinula hilleri.* A. Semidiagrammatic view of right side of animal showing an additional hind gut coil, as well as the position of the stomach with respect to the hind gut. B. Hind gut coils as seen from the dorsal side.

teriorly, and there is a well-developed 'byssal' gland.

Usually there are 9 coils to the hind gut, although we have seen a few whole mounts with 8 or 10 coils. From dissection, we believe that in those which appear to have 8 coils there is a hidden coil, while the single case of 10 coils is an exception to the general rule. The coils, although close together in *S. hilleri*, spread in an overlapping sequence from a point just anterior to the umbo anteriorly to the anterior adductor muscle, the outermost coil abutting the posterior edge of the muscle (Fig. 13). Probably because the hind gut takes up so much anterior space, the stomach and style sac are far posterior within the body and far over on the left side. The stomach in protobranch bivalves is normally situated on the left, but usually not so far to the left as in *S. hilleri*. The first section of the hind gut

lies posterior to the pedal ganglion but barely penetrates the foot below the level of the pedal ganglion (Fig. 13).

Because there are so few large specimens, none were opened to observe the condition of the gonads. However, the smallest specimen to show signs of gonadal development was a male, 2.4 mm in total length. In this specimen, the testis was in a very early stage of development and tenuously covered both the posterior part of the coiled hind gut on the right and the digestive diverticula on the left. There was little development of gonadal tissue in other specimens.

Growth stages from the Angola Basin (Station 195) and the Brazil Basin (Station 156) were examined. The larger specimens from the eastern Atlantic tend to have a sharper rostrum than similar sized specimens from the west (Fig. 14). Slight interpopulation differences in lateral outline did not exceed variation exhibited in a single sample. In the course of growth, the rostrum becomes more pronounced (note a gradual change in the total length/umbo-rostral length ratio, Fig. 15). The postero-ventral margin is more angular in young stages than in older shells, but there is little or no change in the height/length ratio. We have no doubt that the populations of the various basins belong to one and the same species. The larval shell measures 420 μm.

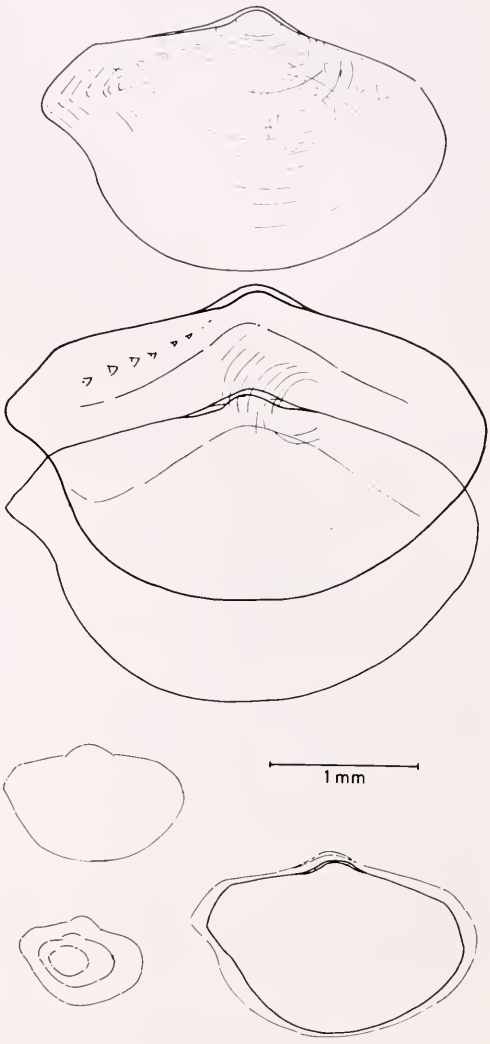

Figure 14. *Spinula hilleri*. Lateral views of a series of specimens to show variations in shell outline, with age and geographical locality.

Spinula scheltemai new species
Figures 16–21 + 28

Holotype: MCZ 279905. (Type locality: ATLANTIS II, Cruise 60, Station 242, Argentine Basin, Lat. 38°16.9'S, Long. 51°56.1'W, in 4382–4405 m.)

Records: Argentine and Guiana Basins. Depth range = 3305–4405 m.

Specific Description. Shell inequilateral, laterally compressed, obliquely oblong/oval in outline, with strong, even concentric lines; rostrum well developed and sharply pointed; umbos anterior and low in profile, very small in larger specimens, more posterior and relatively larger in small specimens, beaks medially directed; except distally, dorsal margin long and relatively straight; antero-dorsal margin slightly convex to about the level of 12th tooth, thereafter sloping abruptly and ventrally to form smooth curve with anterior margin; postero-dorsal margin straight, to level of 10th tooth where it becomes markedly concave, forming the

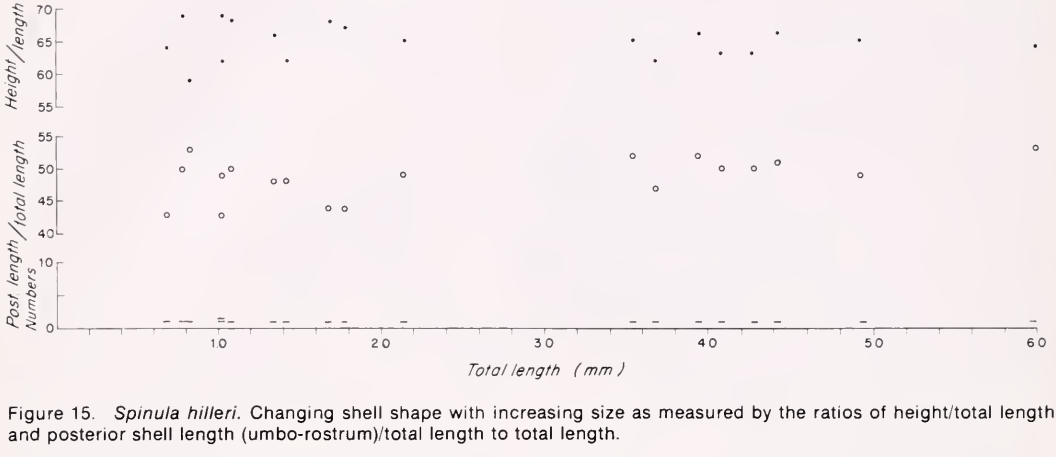

Figure 15. *Spinula hilleri.* Changing shell shape with increasing size as measured by the ratios of height/total length and posterior shell length (umbo-rostrum)/total length to total length.

dorsal side of sharp rostrum; rostrum ventrally concave, remainder of posterior margin broadly truncate; ventral margin long and, except anteriorly, only slightly convex; maximum height of shell well posterior of umbo; well-developed keel close to postero-dorsal margin, less evident near umbo and extending to tip of rostrum, concentric lines making a sharp right angle at keel; hinge plate long and shallow, anterior and posterior plates relatively straight, diverging from dorsal shell margin, anterior hinge plate with 15 small chevron-shaped teeth, posterior plate with 14 small teeth, proximal teeth minute, distal teeth relatively small; ligament amphidetic, inner layer (resilium) wide and lunate, outer layer and periostracum elongate with posterior part slightly longer than anterior and extending beyond posterior hinge plate, anterior part extending to level of 11th tooth. Maximum recorded shell length 11.5 mm.

The present species might superficially be confused with *Spinula oceanica*, which has a somewhat similar shell outline. However, *Spinula oceanica* differs in sculpture, and the anterior dorsal shell margin slopes sharply ventrally immedi-

Table 5. Records for *Spinula scheltemai* new species.

Cruise	No.	Station no.	Depth (m)	No. of specimens	Latitude	Longitude	Gear	Date
				Argentine Basin				
ATLANTIS II	60	259A	3305–3317	5	37°13.3′S	52°45.0′W	ES	26.3.71
ATLANTIS II	60	256	3906–3917	230	37°40.9′S	52°19.3′W	ES	24.3.71
ATLANTIS II	60	242	4382–4405	68	38°16.9′S	51°56.1′W	ES	13.3.71
				Guiana Basin				
KNORR	25	307	3802–3825	10	12°34.4′–12°40.8′N	58°59.3′–59°09.2′W	ES	3.3.72

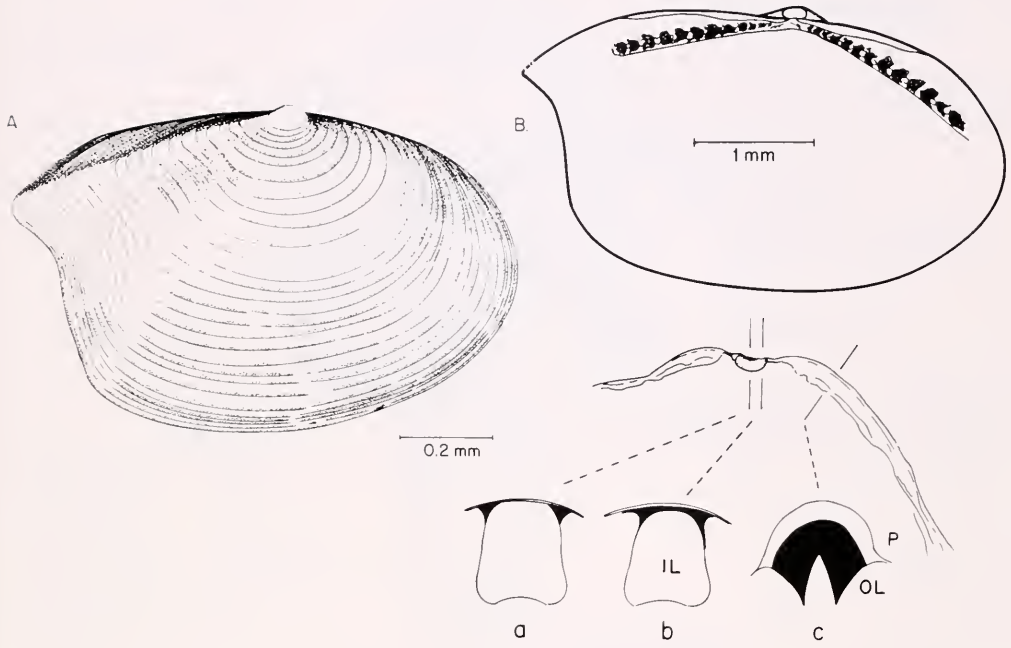

Figure 16. *Spinula scheltemai*. A. External view of right valve of holotype (MCZ 279905) from Station 242. B. Internal view of a left valve from the same station and lateral view of the ligament removed from the hinge plate. a, b, and c, transverse sections through the internal ligament (resilium) and external ligament at the points indicated by the broken lines. *Abbreviations:* P, periostracal layer; IL, inner layer; OL, outer layer.

ately anterior to the umbo. The hinge plate is more slender in *S. oceanica* with the teeth even closer to the dorsal margin. The external ligament is at least twice as long in *S. scheltemai* as in *S. oceanica* and larger than in any other species recorded here.

We name this species after our friend and colleague Dr. Rudolf Scheltema of the Woods Hole Oceanographic Institution.

Morphology. Although the form of the body and mantle is similar to that of other species, the body of *S. scheltemai* occupies more shell space than any other species (Fig. 17). The adductor muscles are much closer to the shell margin, particularly the posterior, possibly because the rostrum of *S. scheltemai* is not greatly extended. The adductor muscles are very large, while the siphonal embayment is short. The anterior sense organ is far anterior in position, but because the adductor muscle lies close to the shell margin, the sense organ is situated immediately below the muscle.

The palps are relatively much larger than in the other species described here. Depending on the size of the animal, 26–50 ridges are present, the palps extending across the entire width of the body. The palp proboscides are very short in the preserved specimens and fill the space between the ventral edge of the gill and the posterior edge of the palp. The gills are moderately well developed with about 25 gill plates to each demibranch. The ganglia are large. A siphonal tentacle inserts either on the left or right side of the base of the siphon. The siphon is moderately large. The gills are attached laterally to the base of the siphon

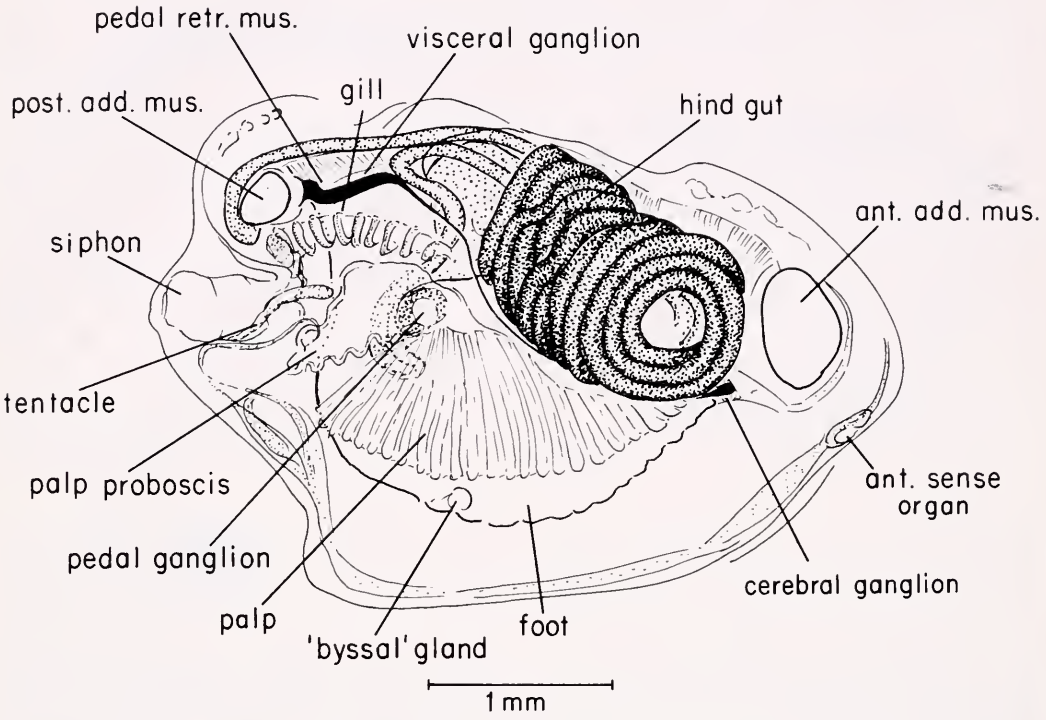

Figure 17. *Spinula scheltemai.* Semidiagrammatic view of the right side of animal to show disposition of organs.

(Fig. 19). The siphon is not obviously a double structure of the type figured by Yonge (1939). It is internally ridged. The mid-lateral ridges, continuations of the gill attachment, are somewhat more obvious than the others. Faecal rods are confined to the dorsal side of the lumen, and probably the internal ridging effectively divides the siphon in two. Dorsally, the siphon is attached by connective tissue that passes postero-lateral to the hind gut.

The gut takes the usual course. Here the mid gut and hind gut penetrate some distance into the foot ventral to the large pedal ganglia. There are 10 coils on the right side of the body, although in most specimens there appear to be only 8. However, sections and whole mounts show that two of the coils may be hidden internal to the tightly packed outer coils. The stomach is large and displaced far to the left side of the body (Fig. 18).

The foot and the 'byssal' gland are well developed. The pedal retractor muscles are similar to those described for *S. filatovae* (p. 7).

There is a change in shape with increasing length (Fig. 20). As in other species, increasing prominence of the rostrum results in a change in position of the umbo relative to the total length. In some cases (Fig. 21) the umbo is posterior to the midline. Total length with respect to height changes but little during the growth of the animals. The smallest specimen showing gonadal development was 2.4 mm total length. Sexes are separate with the larger animals tending to be more mature. No specimen appeared to

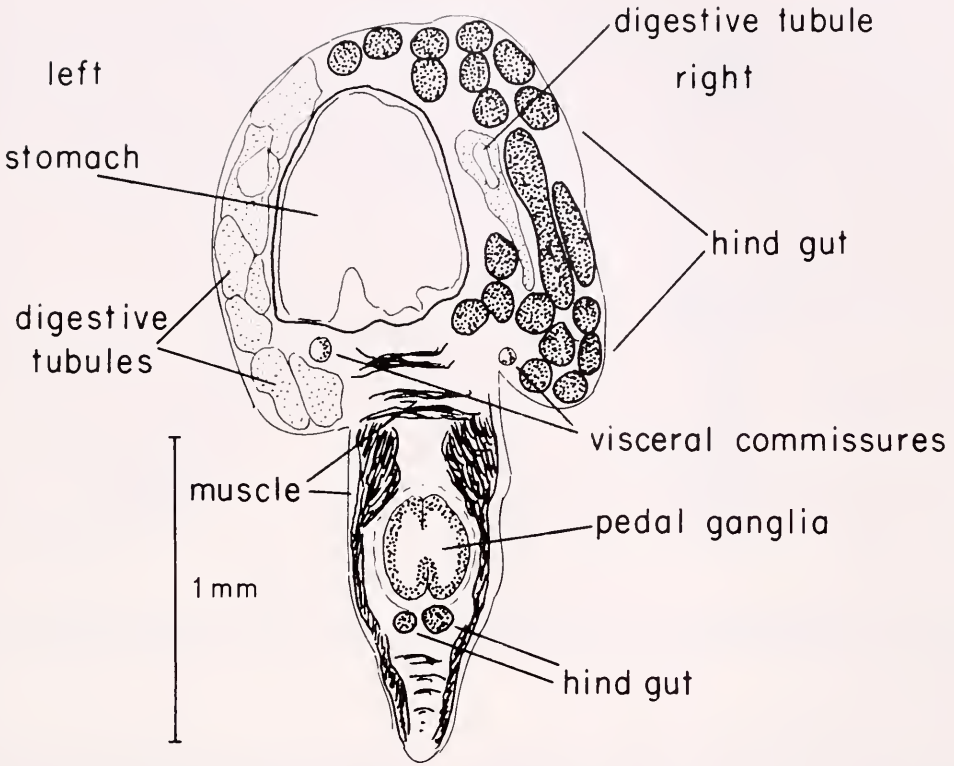

Figure 18. *Spinula scheltemai.* Transverse section through viscera and foot to show position of hind gut and stomach. Pedal ganglia also present with distal end of style sac and proximal end of hind gut in section.

be fully mature. The larval shell measures about 375 μm—the smallest recorded for an Atlantic *Spinula*.

Spinula subexcisa (Dautzenberg and Fischer, 1897)
Figures 22–28

Leda excisa var. *subexcisa* (Dautzenberg and Fischer, 1897: 205. (Type locality: Azores, PRINCESSE-ALICE, Station 69, in 1846 m; type specimen supposedly housed in Institut Oceanographique, Monaco, present whereabouts unknown.)

Previous records (see p. 2): Throughout Atlantic, 1848–5153 m. Probably many previous records have been confused with other species described in this paper. The Norwegian and W. European records can be accepted with some degree of certainty.

Present record: West Europe Basin, 1993 m.

Historical. The first record of *S. subexcisa* was almost certainly that described by Jeffreys (1876, 1879) and incorrectly referred to as *Malletia excisa* (Philippi). The specimens examined by Jeffreys were taken by the PORCUPINE and LIGHTNING expeditions from a position very close to that of the present records for *S. subexcisa*. Jeffreys (1876, 1879), like ourselves, only recognized one species from the area. Jeffreys regarded his specimens as being recent examples of the Sicilian fossil *Nucula excisa* Philippi (1844). As a result he did not figure his specimens, nor did he give a sufficiently accurate description of the specimen to confirm its specific identity. Smith (1885), who identified a specimen as being the same species as that de-

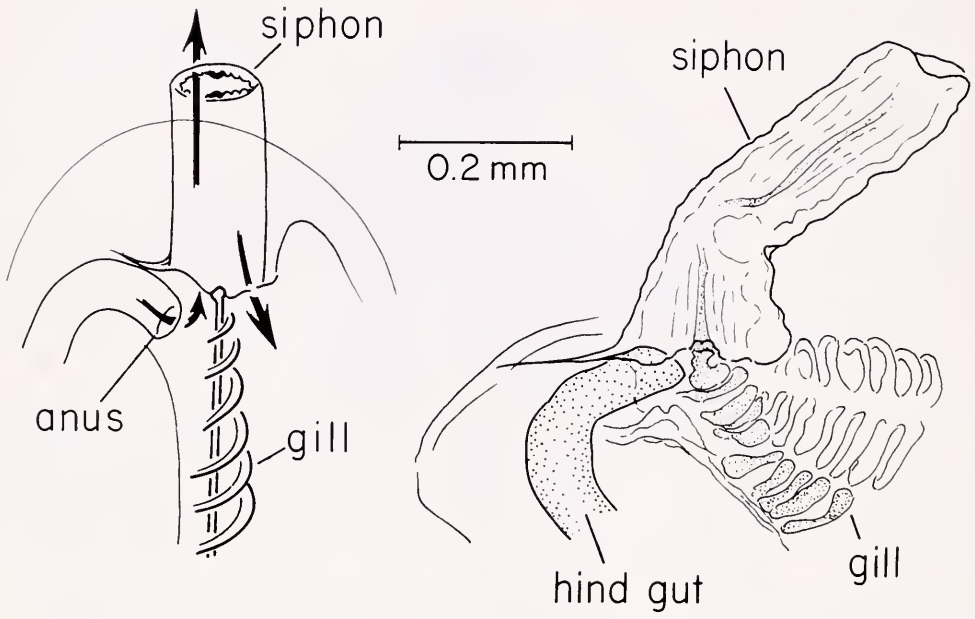

Figure 19. *Spinula scheltemai.* Detail of siphonal region, with diagram to show route of faeces and path of incoming inhalent flow.

scribed by Jeffreys (1876, 1879), reported that its sinus was not as deep as that figured by Philippi (1844). Unfortunately, this unfigured CHALLENGER specimen from the Azores is equally likely to have been a specimen of *S. hilleri* and not *S. subexcisa*. Dautzenberg and Fischer (1897) also came to a conclusion similar to that of Smith (1885) and named their specimens from off the Azores as *Leda excisa* var. *subexcisa*. They gave a somewhat more adequate specific description.

Although we have been unable to examine the specimens referred to above, we have little doubt that our specimens, from almost the same locality where only a single species of *Spinula* is recorded, are the same species that Jeffreys (1876, 1879) examined from the PORCUPINE and LIGHTNING material. Furthermore, the present specimens are certainly not *Leda excisa* (Philippi, 1844), being a totally different shape. They do, however, agree closely with the description of Dautzenberg and Fischer (1897).

Because of the uncertainties in previous descriptions and because the animal itself is not described, we redescribe the species in some detail.

Specific Description. Shell moderately strong, concentric sculpturing somewhat

Table 6. Record for *Spinula subexcisa* (Dautzenberg and Fischer).

Cruise	No.	Station no.	Depth (m)	No. of specimens	Latitude	Longitude	Gear	Date
				West Europe Basin				
CHALLENGER		4	1993	88	56°52.0′N	10°01.0′W	ES	5.6.73

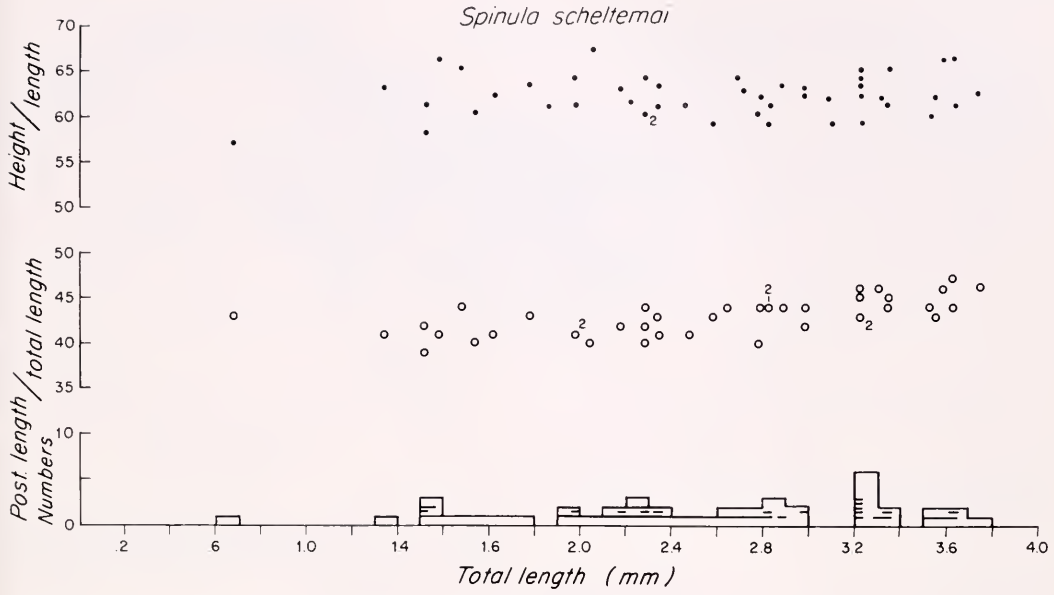

Figure 20. *Spinula scheltemai.* Changing shell shape with increasing size ratios of height/total length and posterior shell length (umbo-rostrum)/total length to total length.

variable both in sharpness of line and in interval; rostrum moderately long and sharply pointed; umbos large, slightly anterior in older specimens, beaks medially curved; dorsal margin sloping gently from the umbo; antero-dorsal margin very slightly convex and forming a smooth curve with anterior margin; postero-dorsal margin very slightly concave to a point immediately posterior to hinge plate where it makes an angle to form the convex dorsal edge of the rostrum, ventral edge of rostrum concave; ventral margin a smooth curve, more convex posteriorly than anteriorly, rostral keel not marked; hinge plate moderately broad distally but coming close to shell margin below umbo, ventral edge of both anterior and posterior hinge plates almost straight; number of teeth varies with size of animal, in largest specimens 11 anterior and 10 posterior teeth—the 6 distal teeth much larger than the rest, those nearest umbo very difficult to distinguish; ligament amphidetic, inner layer

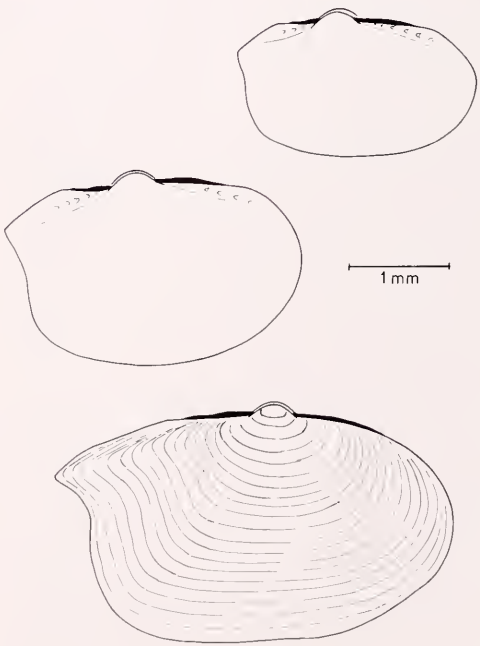

Figure 21. *Spinula scheltemai.* Lateral views of a series of specimens to show change in shell outline with increasing size.

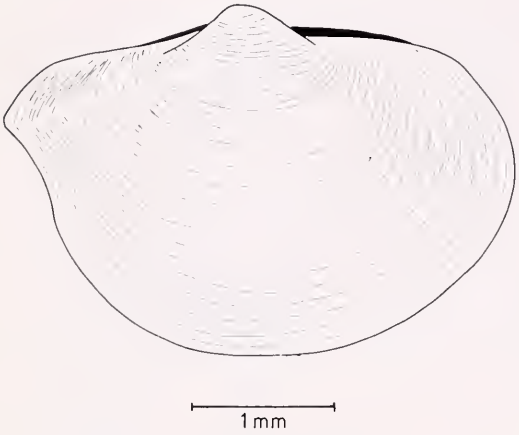

Figure 22. *Spinula subexcisa*. Lateral view of a specimen to show external features of the shell.

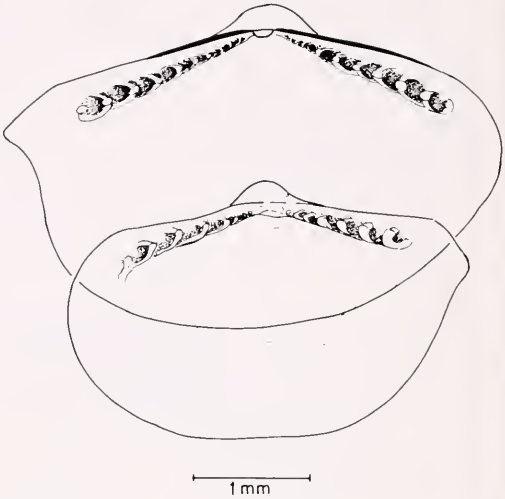

Figure 23. *Spinula subexcisa*. Lateral view of the right and left valves of two different specimens to show shell outline, hinge plate, and differences in tooth number with increasing size of shell.

(resilium) relatively large, oval, occupying width of hinge below umbo, outer layer external and elongate, extending to level of the eighth anterior tooth and seventh posterior tooth in largest specimens. Maximum recorded shell length 4.4 mm.

Spinula subexcisa is very similar in general shape to *S. scheltemai*, but it can be distinguished from the latter species by the smaller number of teeth, the breadth of the hinge plate, the length of the posterior outer layer of the ligament and the less regular, but more closely spaced, concentric sculpture (Figs. 22, 23).

Morphology. The basic form of the body is identical to the other species described here (Fig. 24).

The adductor muscles are unequal in size, the anterior being approximately four times as large as the posterior. The 'quick' and 'catch' sections are clearly visible. The anterior sense organ is far anterior, below but in front of the anterior adductor muscle. The sense organ is particularly well developed, being a semicircular flap of tissue that is an extension of the middle sensory lobe. Underlying the epithelium in this region (both lining the shell and the mantle cavity) is a thick layer of connective tissue with an enlarged space containing the pallial nerve (Fig. 25). The area is also well supplied with glandular epithelial cells, with one well marked dome-shaped patch at the anterior limit of the organ.

The siphon and the feeding aperture are similar to those of other species of *Spinula*. The sensory tentacle lies on the left side at the base of the siphon in most specimens stained as whole mounts.

The palps, with at least 32 narrow ridges, are large and extend the width of the body. The palp proboscides are small and in their contracted state lie between the gill and the posterior rim of the palp. There are 12–18 gill plates in each demibranch; like the palp ridges, the number is dependent on the size of the specimen. As in *S. scheltemai*, the body and foot occupy much of the mantle space. The posterior margin of the foot is extended posteriorly and lies close to the feeding aperture.

As in all species, the mouth is displaced a short distance posterior to the anterior adductor muscle. The course of

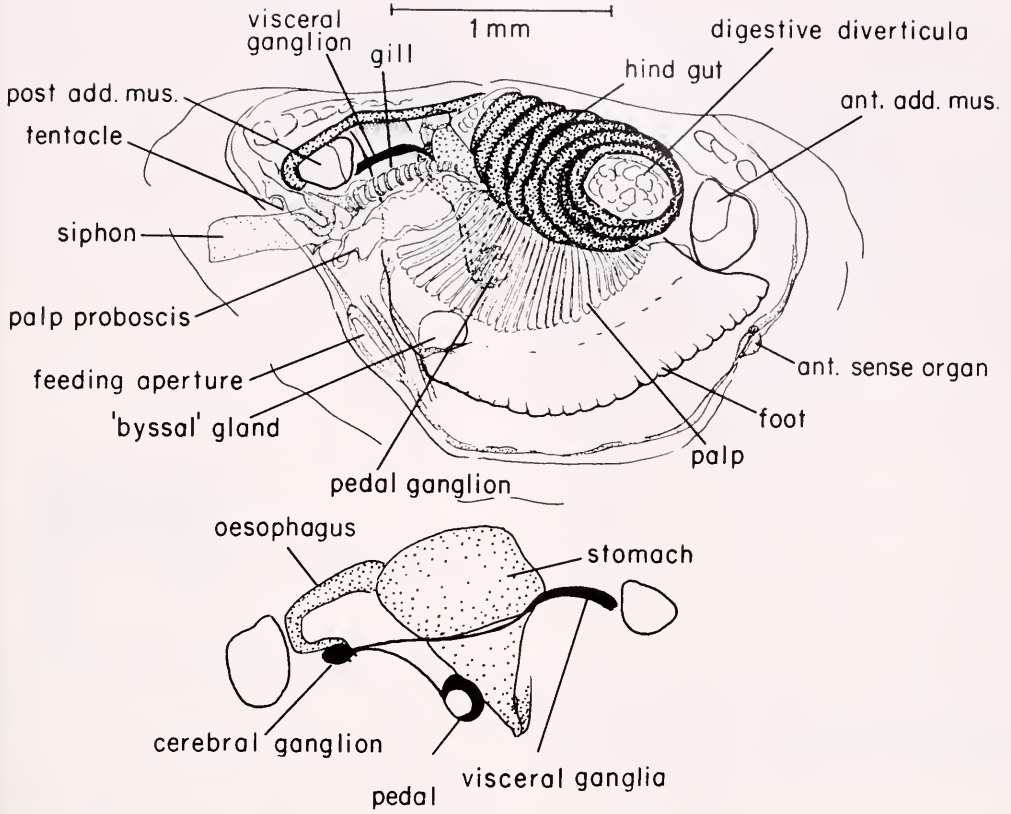

Figure 24. *Spinula subexcisa*. Semidiagrammatic view of right side of the animal to show disposition of organs. Below is detail of stomach and ganglia of the same specimen, but drawn from the left side.

the oesophagus is initially anterior as far as the posterior face of the muscle where it turns posteriorly to join the stomach. The stomach lies posterior and dorsal within the body and is displaced to the left side. On the right there are nine coils of the hind gut. The ganglia are well developed, particularly the pedal, which lies posterior and relatively high in the foot. The foot is not as markedly anterior in its attitude as it is in the more elongate species. The 'byssal' gland is spherical and lies close to the margin of the foot (Fig. 26). The peripheral muscles of the foot form a network around the gland, and appear to form a sphincter at the neck of the gland. The gland itself is composed of hyaline cells. Its function is obscure. As in other protobranchs, no byssus is produced, nor does the gland bear any similarity to the lamellibranch byssus apparatus.

The larval shell measures 450 μm, the largest for an Atlantic species. The juveniles are much more angular than the adults, with rostrum, posterior margin, and antero-dorsal margin combining to give a somewhat elongate, hexagonal appearance (Fig. 27). As growth proceeds, the posterior margin becomes sinusoidal, the rostrum more pronounced, and the anterior margin more rounded.

DISTRIBUTION PATTERNS

Of the five species of *Spinula* recorded from the Atlantic, three species, *S. hil-*

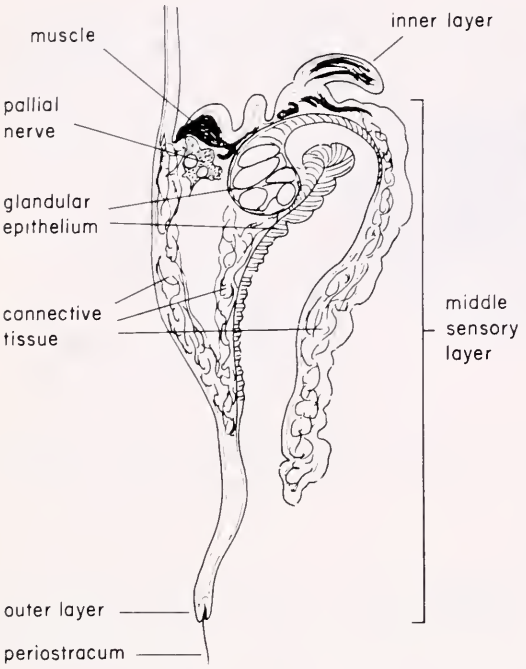

Figure 25. *Spinula subexcisa*. Diagrammatic view of mantle margin cut transversely through the anterior part of the anterior sense organ.

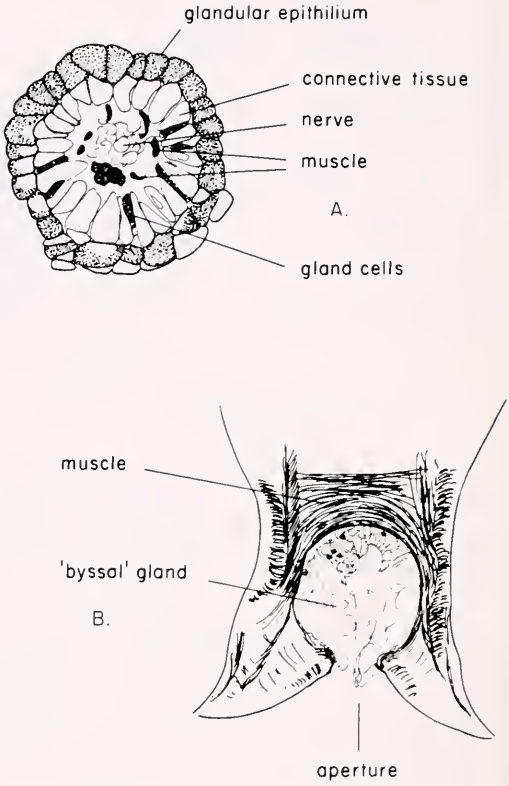

Figure 26. *Spinula subexcisa*. A. Transverse section through sensory tentacle. B. Transverse section through 'byssal' gland and foot musculature.

leri, *S. scheltemai*, and the unnamed species, live in abyssal depths (2500–5000 m), while *S. filatovae* is present at lower slope depths (1200–1800 m), and *S. subexcisa* is probably found on the lower slope and upper abyssal rise (1800–2500 m).

All species, except *S. hilleri*, have somewhat restricted distributions. *S. hilleri* is found in the West Europe, Canary, Cape Verde, Brazil, Angola, and Argentine Basins. It is moderately abundant, numerically forming more than 10% of the protobranch fauna in 3 of the 17 stations where it was found. *Spinula scheltemai* is present in the Argentine and Guiana Basins. In the former basin, it is numerically abundant, forming more than 10% of the protobranchs in two of the three samples that contained it. *S. subexcisa* has been found only in the West Europe Basin where it is a common faunal constituent. In contrast, the unnamed species limited in our samples to the North America Basin, is a rare species. We have collected but a single individual in each of three samples, yet this is one of the most extensively sampled deep-sea basins.

The slope-dwelling species, *S. filatovae*, occurs in the northeastern Atlantic and was present at single stations in the West Europe and Cape Verde Basins, numerically comprising 5% and 6% respectively of the protobranchs in these samples. It occurs at similar depths in the Guinea Basin. Curiously, it is the only species of those described here that, to date, has been recorded outside the At-

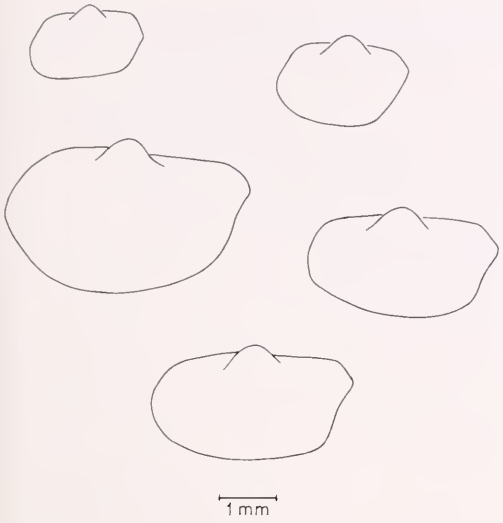

Figure 27. *Spinula subexcisa*. Series of shell outlines in lateral view to show change in shape with increasing size.

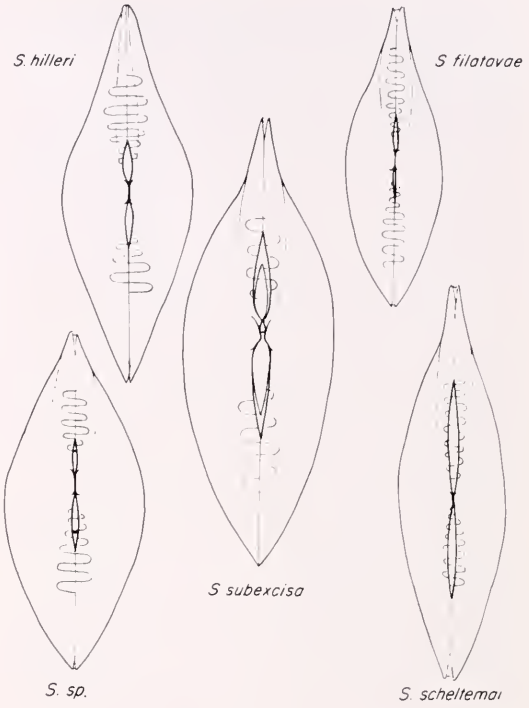

Figure 28. Dorsal view of shell of the five species of *Spinula* from the Atlantic to show differences in shell shape and extent of external ligament.

lantic—a single record from the Gulf of Aden (Knudsen, 1967). Thus, *S. filatovae* may occur along the lower slope of the eastern mid and South Atlantic and extend around the Cape of Good Hope into the western Indian Ocean. Yet, the remarkable differences in the depth records for this species in the Atlantic (1261, 1376, 1624–1796, and 1739 m) as compared to the Indian Ocean and Gulf of Aden (2312, 3152–3202, 3546, 4300–4340, and 4314–4324 m), together with the absence of any detailed knowledge of the soft part anatomy for the Indian Ocean specimens, raise the possibility that we may unwittingly be lumping together two morphologically similar species. *S. filatovae* appears to be absent from the western Atlantic.

MORPHOLOGICAL CONSIDERATIONS

Both the shell and soft parts of species in the genus *Spinula* are amazingly conservative. Of the species recorded from the Atlantic, specific shell differences are a matter of subtle variations in shape and dimension. At one extreme there is a bivalve with a robust broad hinge with heavy teeth (Figs. 11, 28) combined with small adductors (Fig. 12) and a relatively short amphidetic ligament without a strongly developed outer layer (Fig. 28). At the other extreme there is a bivalve with a less robust, slimmer hinge with finer, more numerous teeth (Fig. 16), large adductors (Fig. 17), and a well-developed elongate, arched outer layer to the ligament (Fig. 28). The latter type of ligament is reminiscent of the external ligament (albeit opisthodetic) of the Tellinacea. Possibly the analogy can be stretched further to suggest that *Spinula* is the deep-sea, deposit feeding, counterpart of *Tellina*, a slender, active deep burrowing, deposit feeder.

This view is reinforced by various points of morphology. *Spinula* is well endowed with large ganglia, particularly the pedal; the foot is very elongate and

muscular, somewhat anteriorly directed, particularly in the elongate species, and the viscera do not penetrate it to any great degree; the siphon is long and muscular; the adductor muscles, although unequal, are powerful with clearly defined 'quick' and 'catch' parts; and the anterior sense organ is far anterior. All these features suggest that *Spinula* is an active burrowing infaunal bivalve.

Other characteristics typical of deep-sea genera (Allen, 1975) are the large, finely-ridged palps and the relatively small gills with few gill plates. *Spinula filatovae*, the slope species, has the largest number of gill plates and the smallest palp with relatively few palp ridges. *Spinula hilleri*, *S. scheltemai*, *S. subexcisa*, and the unnamed species are remarkably alike with respect to gill and palp morphology. Similarly, in *S. filatovae* the hind gut, although much coiled, is relatively small in diameter, the coils being mostly laid on top of one another, while in the other four species the coils tend to be overlapping and with a much wider lumen. The number of coils varies: *S. filatovae* (6), the unnamed species (7), *S. subexcisa* and *S. hilleri* (9), and *S. scheltemai* (10), with occasional variation within species. Increase in gut volume and length with increasing depth is well known in bivalves. Although not so well defined in terms of increasing number of coils with increasing depth distribution, this principle still holds in general terms for the genus *Spinula*. The Pacific species *S. tasmanica* (6), *S. vityazi* (7), and *S. kermadecensis* (7) possibly have fewer coils, but further investigations might show additional hidden coils beneath those closely packed coils at the surface. The exception to the general rule of a multiple-coiled hind gut on the right side of the body is *Spinula calcar* (4063–6096 m) (Dall, 1908). It has one hind gut loop on the right side of the body, which is the primitive condition in protobranch bivalves. It seems that the morphology and taxonomy of this species should be re-examined.

Spinula is clearly adapted to deal with large quantities of sediment entering the mantle cavity. Judging from the extension of the posterior margin of the foot, unwanted sediment is thrust out of the feeding aperture by the heel. It is possible that the 'byssal' gland secretes an adhesive fluid to bind unwanted particles together before they are rejected. It is strategically placed and of a large enough size in *Spinula* to perform this function. In addition, there are large numbers of mucous glands present in the region of the feeding aperture. However, these may be more concerned with the processing of incoming particles on the palp proboscides than with outgoing pseudofaeces.

The unequal size of the adductor muscles, *not* associated here with anterior enlargement of the mantle cavity, may serve to prevent the combined siphon, on the occasion of its retraction, from being trapped by the closing valves. It may also serve to assist in clearing large quantities of pseudofaecal material. Certainly, large amounts of sediment are present in the posterior part of the mantle cavity of many specimens. However, the very nature of the methods of collection prevents any emphatic and significant conclusion from being drawn.

The sediment in the gut is very fine and, for the most part, is composed of fragments of diatoms and foraminiferans. It is difficult to say whether these fragments are in any way concentrated or selected.

Although the larval shell indicates a large egg, there is no evidence of direct development. For the most part, our samples show either immature or only partially mature animals. Sexes are separate. The most mature animals are among the largest, and the picture presented is similar to the one seen in the case of *Tindaria*. Whether or not *Spinula*, like the

latter genus, is long-lived (Turekian *et al.*, 1975) will have to await dating by radio-chemical methods.

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Relationships of the Stomiiform Fishes (Teleostei), with a Description of *Diplophos*

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RELATIONSHIPS OF THE STOMIIFORM FISHES (TELEOSTEI), WITH A DESCRIPTION OF *DIPLOPHOS*

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STANLEY H. WEITZMAN[2]

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ABSTRACT. A primarily osteological description is provided for two species of the phylogenetically and morphologically primitive stomiiform teleost genus *Diplophos*. Evidence is presented to document the monophyly of two major teleostean groups, the Stomiiformes and the Neoteleostei. Monophyly of the Eurypterygii (*sensu* Rosen, 1973) is evaluated and tentatively accepted. Stomiiforms, previously placed by most authors as a suborder (Stomiatoidei) of the Protacanthopterygii, are found to be neoteleosts; they comprise the sister group of all other neoteleosts, the Eurypterygii. The Protacanthopterygii (comprising the Esocoidei, Argentinoidei, and Salmonoidei, including the Salmonoidea and Osmeroidea, *sensu* Rosen, 1974) is not supported as monophyletic. Alternative hypotheses of "protacanthopterygian" relationships are suggested and discussed.

INTRODUCTION

The group of teleosts herein termed Stomiiformes comprises a significant portion of the oceanic vertebrate fauna. The group consists of mesopelagic and bathypelagic fishes and currently includes 9 families, 50 genera, and over 300 species. Stomiiforms are found in all of the major ocean basins; adults range in size from about 15 mm to nearly 500 mm in length. The group has been the subject of extensive research, including distributional studies and systematics at all taxonomic levels (e.g., Baird, 1971; Baird and Eckardt, 1972; Gibbs, 1969; Goodyear and Gibbs, 1970; Morrow and Gibbs, 1964; Mukhacheva, 1978; Parin *et al.*, 1977; Parin and Pokhilskaya, 1974, 1978; Weitzman, 1967a, b, 1974), studies in photobiology and vision (e.g., Baguet and

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Marechal, 1976; Fernandez, 1978; Hansen, 1970; Jørgensen and Munk, 1979; Lockett, 1977; O'Day, 1973), in ecology (e.g., Clarke, 1974, 1978; DeWitt and Cailliet, 1972; Hopkins and Baird, 1973; Merrett and Roe, 1974), in biochemistry and physiology (e.g., Blaxter *et al.*, 1971; Childress and Nygaard, 1973; Douglas *et al.*, 1976), and in fisheries (e.g., Gjøsaeter and Kawaguchi, 1980). The degree of morphological diversity and extent of specialization in body form and feeding structures makes the group an excellent model for studies concerned with evolution in general, but especially evolution in the oceanic environment.

It is becoming widely accepted that phylogenetic analyses of relationship are crucial to and must precede explication of evolutionary patterns and subsequent discussions of evolutionary mechanisms (e.g., Eldredge and Cracraft, 1980; Lauder, 1981; Wiley, 1981). Only recently have explicitly phylogenetic methods been used to elucidate relationships within the Stomiiformes (Weitzman, 1974; Fink, 1976, and in preparation). The phylogenetic relationship of the Stomiiformes to other teleosts has been examined by Rosen (1973). In order to facilitate future phylogenetic and evolutionary studies on the group, we reconsider stomiiform relationships *vis à vis* other teleosts and provide a diagnosis of the group using phylogenetic methodology.

The nomenclature used herein reflects the findings of Steyskal (1980) regarding formation of suprageneric names based on the name *Stomias*. Steyskal (p. 172) found that the traditional usage, such as Stomiatidae or Stomiatiformes (Rosen, 1973), is incorrect and these names should be amended to Stomiidae and Stomiiformes, following the International Code of Zoological Nomenclature.

There are three major sections to this paper. First, there is an osteological description of specimens of *Diplophos*, which we consider representative of phylogenetically and morphologically primitive stomiiforms (see Fig. 1). Second, we present evidence bearing on the monophyly of the Stomiiformes and on the relationships of the group with other teleosts. Finally, we evaluate recent hypotheses of relationships within the Protacanthopterygii based on the evidence we have encountered during our investigation of stomiiform relationships.

Our recognition of *Diplophos* species as representative of morphologically and phylogenetically primitive stomiiforms is based on outgroup comparisons. We surveyed the morphology of members of the Stomiiformes and of numerous primitive teleosts in order to determine the distributions of traits among them. The stomiiform genus whose members share the fewest characters with other stomiiforms and thus the most characters with other primitive teleosts is *Diplophos*. It is possible that *Diplophos* is not monophyletic, since no derived characters have ever been used in its diagnosis. Should the genus be monophyletic, the character distribution we find suggests that *Diplophos* is the sister group of all other stomiiforms; however, a documented statement of that hypothesis and a diagnosis of the genus is not included herein, pending further work on the genera included by Weitzman (1974) in the Gonostomatidae and Photichthyidae. Our study does not include a critical examination of those families (which were not diagnosed by Weitzman), and *Diplophos* may eventually be found to be a member of some primitive stomiiform subgroup. However, the usefulness of *Diplophos* species as representative of relatively primitive stomiiforms is not dependent upon precise hypotheses of their phylogenetic relationships. The four known species of *Diplophos* have been examined by us and were reviewed by Mukhacheva (1978).

Our concept of relationships is phylogenetic (*sensu* Hennig, 1966). Use of the word primitive in the text, unless other-

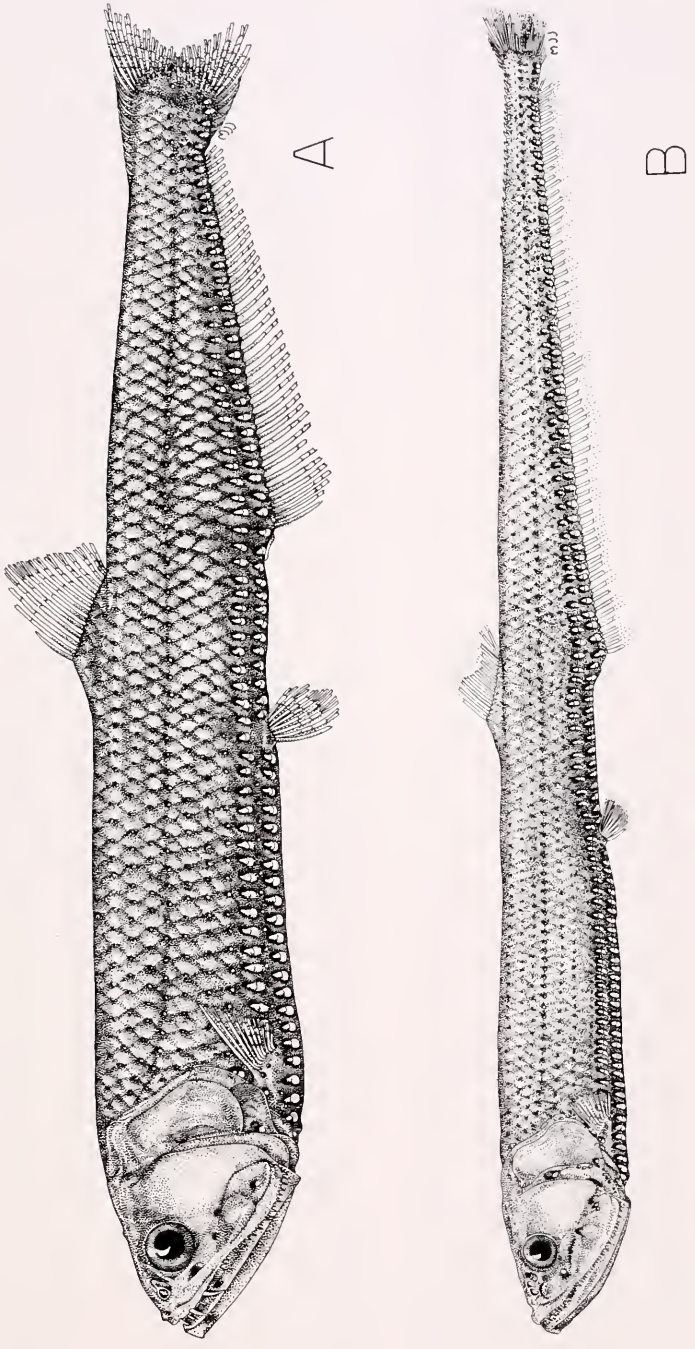

Figure 1. A. *Diplophos maderensis* (USNM 186364; 114.0 mm SL). B. *Diplophos taenia* (USNM 203292; 83.4 mm SL).

wise qualified, refers to phylogenetically primitive. Characters used to diagnose groups (synapomorphies) were chosen by comparison with numerous species in appropriate outgroups. Specimens examined are listed in the Appendix.

In later sections we present arguments for use as synapomorphies certain similarities among the various teleosts discussed. We have concentrated our search for characters and the discussion below on what we believe to be primitive members of their lineages, based on outgroup comparisons. We surveyed more derived members of each group, as well, to try to ensure that the characters we were using as synapomorphies for each lineage were not instead synapomorphies for some relatively primitive subgroup within that lineage. Also, we have tried to point to instances of "convergence," when characters used as synapomorphies for a group also appear to be present in other lineages. Recognition of convergence is based on parsimony criteria, and our justification is presented for each case.

We have not utilized evolutionary "trends" or "tendencies" as characters. Usually implicit in these concepts is the assumption that primitive members of the group lack a character while more derived members have it. In such a case, however, presence of the character would actually diagnose some subgroup(s) within a larger group. When a character "trend" is based on a character which is present but less elaborated in primitive members, we would use presence of the character in its primitive form to diagnose the group and presence of the more elaborated character to diagnose a subgroup.

Rosen's conclusion (1973), with which we agree, that stomiiforms represent a lineage separate from the Protacanthopterygii, in which the "Stomiatoidei" has generally been placed, required a change to ordinal rank for the group. This would seem to necessitate comparable changes in rank for many of the groups recognized by Weitzman (1974), but we prefer to retain his ranking of taxa at the infraordinal level and below, pending work on relationships of the genera of primitive stomiiforms and publication of the senior author's work on the "Stomiatoidea."

In the description of *Diplophos*, bones are listed as paired or unpaired; descriptions of paired bones are for one member of the pair.

Most of the specimens used in this study were cleared and stained, using a modified version of the enzyme technique of Taylor (1967). The illustrations were prepared with the use of camera lucida with Wild M-5 or Zeiss IV-B Zoom microscopes; a Leitz Widefield stereomicroscope was used for detailed observations.

DESCRIPTION OF *DIPLOPHOS*

Ethmoid Region

The ethmoid cartilage forms the core of the anterior region of the neurocranium (Figs. 2–4). In dorsal view, the ethmoid cartilage has three major features: an anterior, broad lateral concavity, the lateral prenasal process, and a deeply concave recess for the nasal capsule. In dorsal view the profile of the anterior border of the ethmoid cartilage lies at about a 90° angle to the longitudinal body axis, paralleling the anterior border of the vomer. At the midline, the ethmoid cartilage is dorsoventrally shallowest anteriorly, gaining in thickness posteriorly, and reaching its greatest thickness just posterior to the level of the lateral prenasal processes. There are two major lateral extensions of the ethmoid cartilage: the lateral prenasal processes and the lamina orbitonasalis. Anterior to the prenasal processes, the anterodorsal ethmoid surface is broadly concave, forming an articular surface for the maxilla. Between the prenasal process and the lamina orbitonasalis is the deeply concave olfactory recess. Within the posterior wall of the olfactory recess is the foramen

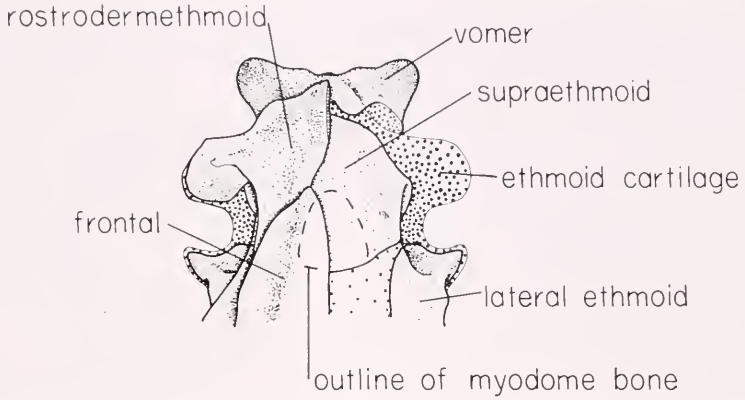

Figure 2. Ethmoid region of *D. taenia* (USNM 206614; 171.0 mm SL), dorsal view; right portion of rostrodermethmoid removed.

olfactorium advehens, through which the olfactory nerve passes. The posterior surface of the ethmoid cartilage has a single, medial deep conical recess, the anterior myodome, in which the superior oblique eye muscles have their point of origin. Posterior to the lamina orbitonasalis, the cartilage is continuous with the trabeculum communis (Fig. 5) ventrally and the orbital cartilages dorsally. The trabeculum communis extends posteriorly from the ethmoid cartilage and lies just dorsal to the parasphenoid bone. A membraneous interorbital septum extends from the trabeculum communis to the frontal bones above the orbit.

The ethmoid ossifications include a single supraethmoid, a single rostrodermethmoid, a single ventral ethmoid, paired lateral ethmoids, and a single anterior myodome bone. The supraethmoid is a perichondral ossification on the dorsal cartilage surface. Posteriorly, the supraethmoid has a slightly convex border, and its lateral edges meet the posteromedial borders of the olfactory recesses. Anteriorly, the supraethmoid border is more convex than the posterior border, and its lateral edges meet the anteromedial border of the olfactory recesses. The supraethmoid ossification also covers the medial surface of the olfactory recess as the capsular portion of the supraethmoid. This capsular portion, primarily endochondral, is an approximately cone-shaped object with its apex near the dorsal midline. Laterally, the capsular portion is highly fenestrated. (In some more specialized stomiiforms and in the osmerid *Spirinchus*, the capsular portion of the supraethmoid is separate from the dorsal portion; Weitzman, 1967: 509, Fig. 1.)

The dermal rostrodermethmoid is a bone formed by fusion of the paired dermethmoids with the single rostral (Patterson, 1975: 511). The anteromedial "rostral" section extends anterior to and between the "dermethmoid" portions. Thus, there is a medial ramus between the dermethmoid portions which extends a distance about equal to one-quarter of their length in an anteroposterior axis. Each lateral portion of the ossification is essentially composed of two large rami, both of which partially overlie the supraethmoid. The lateral ramus is fenestrated, with its anterior border overlying the anterior border of the ethmoid cartilage and its posterior border overlying the anterior border of the olfactory recess; its lateral apex reaches near the lateralmost border of the prenasal process of the ethmoid cartilage. The posterior

rostrodermethmoid ramus is smooth and extends posteriorly to overlap the frontal. The lateral border of the posterior ramus overlies the medial border of the olfactory recess; the medial border is slightly convex and extends towards the midline to the point where the posterior rami of the rostrodermethmoids meet. The posterior ramus reaches to a point just dorsal to the vertical ramus of the lateral ethmoid. Anteriorly, the rostral portion reaches very near to the vomer.

Weitzman (1967a) considered the presence of two, separate "proethmoids" (= lateral dermethmoids of Patterson, 1975) to be primitive within the Protacanthopterygii. However, Patterson (1975: 511–512) found that fusion of the rostral and lateral dermethmoids into a single bone (the rostrodermethmoid) is primitive within teleosts. In most teleosts the ethmoid commissure is absent, but in *Megalops*, at least, it is present (see Patterson, 1975, Fig. 140). We agree with Patterson that the presence of two separated "proethmoids" of some osmeroids and stomiiforms is a derived feature. We further suggest that "proethmoids" result from reduction or loss of the rostral portion of the rostrodermethmoid. This loss has occurred independently in osmeroids and stomiiforms, since in *Diplophos* and some other primitive stomiiforms such as *Gonostoma*, *Photichthys*, and *Triplophos*, and in some osmeroids such as *Hypomesus*, there is a single rostrodermethmoid. In *Osmerus* (MCZ 56535) we find the two "proethmoids" as described by Weitzman (1967a: 509), but in addition find a small but well-developed triangular ossification lying anteromedial to the "proethmoids"; we take this small bone to be the rostral element. In a post-larval specimen of *Diplophos taenia* (34 mm SL; MCZ 52548), we see what appears to be a small, chevron-shaped ossification lying adjacent and anteromedial to the lateral dermethmoids; we are unable to clearly discern joint lines completely around this ossification, but propose that it is the rostral element which is partially (or completely?) joined to the lateral dermethmoids.

The conclusion that we have reached regarding the phylogenetic history of the lateral and rostral dermal ethmoid ossifications leads us to call the lateral ossifications lateral dermethmoids rather than proethmoids (as done by Weitzman, 1967a). This more clearly indicates their homology with the lateral dermethmoids of primitive teleosts.

Also, *contra* Weitzman's (1967a: 519) statement that the "lateral supraethmoid process" (=rostrodermethmoid, herein) is fused to the supraethmoid in large specimens of *Polymetme*, we find the rostrodermethmoid autogenous in specimens of *Polymetme* that we have examined, but note that the bones are indeed tightly joined in adults.

The ventral ethmoid is a single, median perichondral ossification that lies dorsal to and fuses with the vomer during ontogeny. The anterior border of the ventral ethmoid lies ventral to the anterior border of the ethmoid cartilage; in that area, in adults, the ossification is fused to the vomer. There are bilateral, posterolaterally projecting broad rami, almost triangular from ventral aspect, which extend over most of the dorsal surface of the vomer, and beyond the border of the vomer, posterolaterally.

The anterior myodome bone lines the conical myodome cavity in the posterior wall of the ethmoid cartilage. The ossification extends anteriorly to a point near the anteromedial apices of the capsular portions of the supraethmoid. The posterior border expands to near the level of the posteroventral border of the capsular portion of the supraethmoid, and ventrally to the level of the posterior border of the supraethmoid.

The lateral ethmoids are paired, perichondral ossifications. The following description is of one side only, but applies equally to the other. The bone covers the anterior and posterior surfaces of the lam-

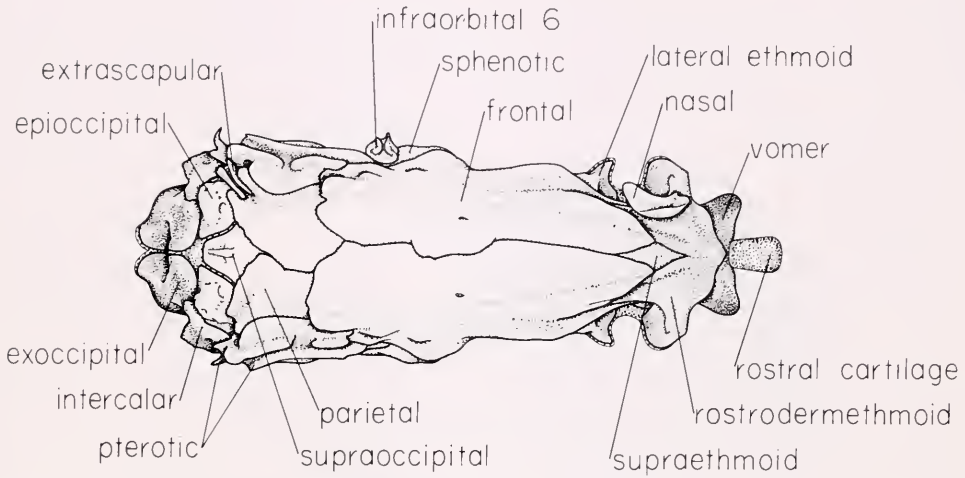

Figure 3. Neurocranium of *D. taenia* (USNM 206614; 171.0 mm SL), dorsal view. Infraorbital 6 = dermosphenotic of authors.

ina orbitonasalis, thus lining the posterior wall of the nasal capsule and the anterior wall of the orbit. Within the nasal recess, the lateral ethmoid ossification extends to the lateral border of the foramen olfactorium advehens and is continuous through the lateral wall of the foramen with the ossification on the posterior wall of the lamina orbitonasalis. Anterodorsally the lateral ethmoid extends to a point about one-third of the way around the concave dorsoposterior border of the olfactory recess. Posteriorly, the lateral ethmoid ossification extends about one-fourth the length of the dorsal wall of the orbital cavity.

The vomer (Figs. 2–4, 13) is a median bone which lies ventral to the ethmoid cartilage. It is a compound bone composed of the ventral ethmoid and vomer proper (see ventral ethmoid, above). Anteriorly the vomer is relatively wide, with two broad lateral rami which anteriorly lie ventral to the anterior border of the ethmoid cartilage. Each ramus has one to three conical teeth ankylosed to it laterally (Fig. 4). Anteromedially the vomer extends dorsally over the anterior border of the ethmoid cartilage to nearly reach the rostrodermethmoid, to which it is tightly bound by thick connective tissue. Posteriorly, the vomer tapers to an elongate, sharply-pointed median ramus that extends to about the level of the anterior wall of the orbit and is enclosed dorsally by the parasphenoid. A thick median fibrocartilage body, the rostral cartilage, lies between the anterodorsal surface of the ethmoid region and the posterior surfaces of the premaxillary bones.

Frontal and Parietal

The frontal bones are paired dermal ossifications that form the major portion of the skull roof (Figs. 3, 4, 6). Anteriorly the frontal extends partially over the ethmoid cartilage, reaching a point about equal to the anterior extension of the anterior myodome bone. Anterolaterally the frontal lies dorsal to the medial border of the nasal recess and dorsal to the lateral ethmoid. More posteriorly, the frontal overlies the tectum cranii and forms the lateral border of the skull roof and the dorsal border of the orbit. At the posterodorsal border of the orbit, the frontal curves medially, with its posterior border ranging in various individuals from deeply convex to relatively straight,

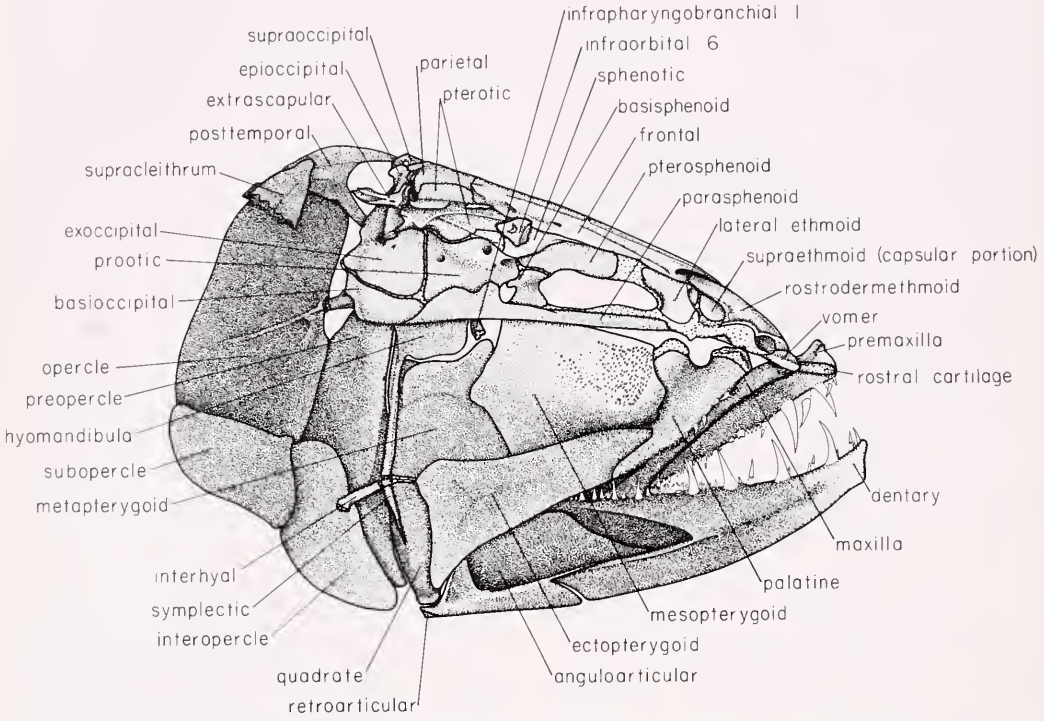

Figure 4. Neurocranium (lateral view) and suspensorium (medial view) of *D. taenia* (USNM 206614; 171.0 mm SL). Infraorbital 6 = dermosphenotic of authors.

at about a 90° angle to the longitudinal body axis. The posterior frontal border lies at a point about one-fifth the length of the neurocranium from its posterior border. Medially, the frontals meet in an irregular articulation and partially overlap one another. The frontals partially overlie the following bones: supraethmoid, lateral ethmoids, sphenotics, pterotics, and parietals.

The supraorbital sensory canal lies on the dorsal surface of the frontal and is enclosed in bone for about one-third its length in small specimens and is nearly enclosed for much of the length of the frontal in large specimens.

The parietals are paired dermal ossifications forming the dorsal surface of about the posterior quadrant of the neurocranium (Figs. 3–7). The parietal is roughly square in dorsal view. The anterior border lies ventral to the frontal, is irregular, and lies at approximately a 90° angle to the longitudinal body axis. The lateral border is superficially overlain by the pterotic and lies more or less parallel to the longitudinal body axis. Just lateral to the mid-length of the parietal, there is a deep concave facet in which the pterotic articulates. There is a deep notch in the posterolateral border for passage of a sensory canal. The posterior parietal border articulates with the epioccipital posterolaterally and with the suraoccipital posteromedially. The parietals broadly overlap at the dorsal midline.

Pterosphenoid, Sphenotic, Parasphenoid, Basisphenoid, and Posterior Myodome

The pterosphenoids are paired ossifications that form the posterodorsal wall of the orbits (Figs. 4–6). There is an an-

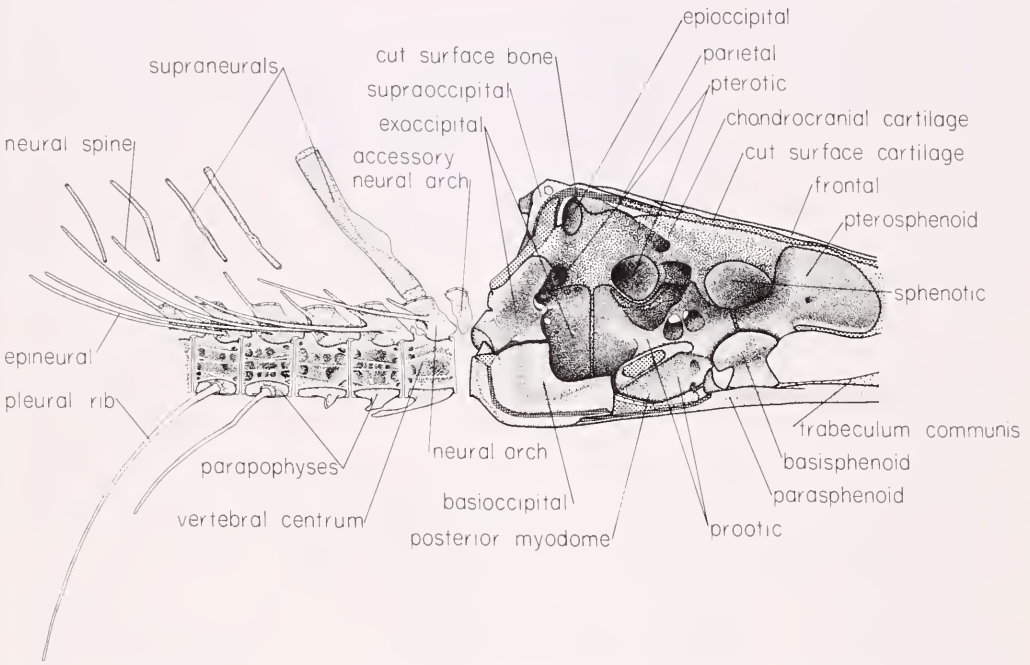

Figure 5. Neurocranium (internal view) and anterior vertebrae (lateral view) of *D. taenia* (USNM 206614; 171.0 mm SL).

terior perichondral portion that encloses much of the orbital cartilage. The pterosphenoid reaches a level just anterior to the midpoint of the orbit. Anteroventrally there is a synchondral joint with the contralateral pterosphenoid; posteroventrally there is a synchondral joint with the basisphenoid. The dorsal perichondral border is very broadly convex; posteriorly it articulates synchondrally with the prootic; posterodorsally it articulates synchondrally with the sphenotic; dorsally it approaches or articulates with the frontal. Anterodorsal to its articulation with the basisphenoid, the pterosphenoid has a deep concavity which forms the dorsal border of the optic foramen.

In medial aspect the pterosphenoid forms the floor and ventrolateral walls of the cranial fossa (Figs. 5, 6). The dorsal surface of the bone is shallowly concave anteriorly and posteriorly; between these concavities the bone has a small dorsal rise that extends dorsolaterally.

The sphenotics are paired bones, posterolaterally articulating synchondrally with the pterosphenoids and anterolaterally articulating synchondrally with the prootics; they form the posterolateral border to the orbital fossa (Figs. 3–6). Anteriorly the sphenotic lies more or less horizontally, with vertical perichondral ossifications lining the posterodorsal roof of the orbital fossa and dorsal ossifications forming the lateral border of the neurocranium (the sphenotic is almost completely overlain by the frontal). The posterior half of the sphenotic extends more ventrally and medially than the anterior half; it extends ventrally to join the prootic synchondrally and (endochondrally) extends medially to form part of the lateral wall of the cranial fossa (Fig. 5). The posteroventral border of the sphenotic is slightly to deeply concave; medial to this concavity is the articulation of the hyomandibula (the hyomandibular fossa). In medial aspect, the

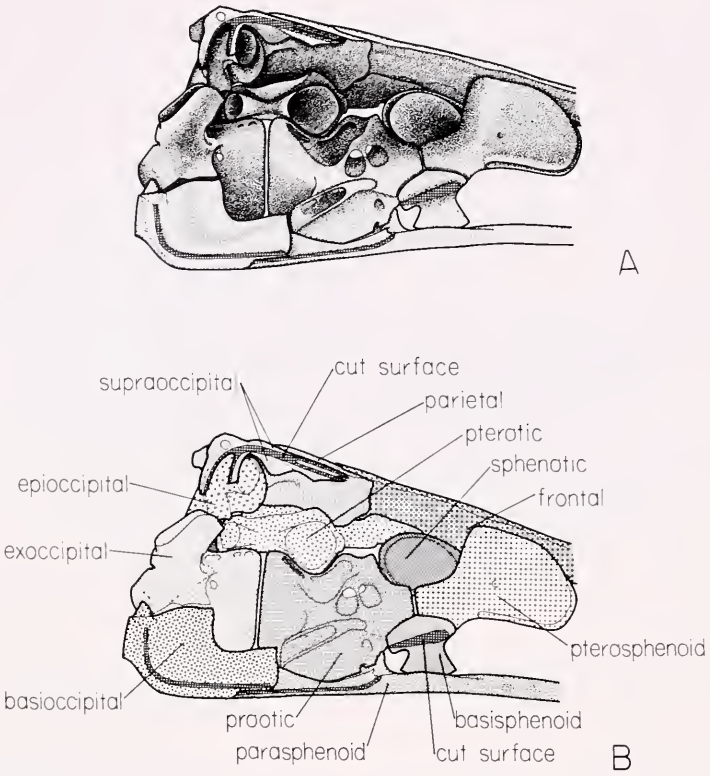

Figure 6. A. Neurocranium of *D. taenia* (USNM 206614; 171.0 mm SL), internal view; cartilage not shown. B. Same as A, with each bone represented by a symbol pattern.

sphenotic is deeply concave; posteriorly, there is a small conical fossa against which lies the anterior portion of the anterior vertical semicircular canal. In *D. maderensis*, *D. greyae*, and *D. rebainsi*, the cartilaginous chondrocranium lies between the sphenotic and the brain cavity; in *D. taenia*, no cartilage is present in that area and bone is visible on the medial surface of the braincase (Fig. 5).

The parasphenoid is a single, relatively straight median bone (Fig. 4). Anteriorly, the parasphenoid lies just ventral to the ethmoid cartilage, approaching its anterior border. More posteriorly the parasphenoid extends ventral to the trabeculum communis to form the medial floor of the orbit. The ventral surface of the parasphenoid is concave in the region ventral to the posterior areas of the ethmoid cartilage and orbit; the vomer articulates in this concavity. At a point about the mid-length of the orbit (in *D. maderensis*) or posterior to that point (in *D. taenia*) there is a bilateral flange of bone that enlarges posteriorly; each flange extends up to meet and lie lateral to the basisphenoid and then continues as a lateral wing that lies lateral to and is tightly articulated with the prootic and basioccipital. The posterior extension of the parasphenoid lies medial to about the midpoint of the otic bullae.

The basisphenoid consists of a single ventral ramus and broad, short bilateral dorsal rami (Figs. 4–6). The ventral ramus extends over the trabeculum communis and enters the orbital cavity; the ventral border of the basisphenoid ossification is either slightly convex or more

or less straight and horizontal, curving dorsally anteriorly, and reaching to about the level of the dorsal border of the lateral parasphenoid wing. The dorsal rami extend laterally, anterodorsally articulating synchondrally with the pterosphenoids posterodorsally and posteriorly lying medial to and articulating diarthrally with the prootic. From lateral aspect the anterior basisphenoid border is concave, the posterior border more deeply so; the dorsal border is broadly convex (see Figs. 5, 6). The anteromedian border of each lateral ramus is deeply concave and forms the ventral border of the optic foramen. Between the posterior border of the ventral basisphenoid ramus and the prootic and parasphenoid, there is a hiatus; in more derived stomiiforms this hiatus is relatively large and is termed the post-basisphenoid space of Weitzman (1967a).

The medial surface of the basisphenoid, facing the cranial fossa, is deeply concave.

The posterior myodome is relatively large and deep (Figs. 5, 6). Anteriorly the myodome extends dorsally as far as the dorsoventral surfaces of the lateral basisphenoid rami. Posteriorly, the dorsal roof of the myodome is formed by the medial prootic laminae. The floor of the myodome is formed by the parasphenoid and its lateral extensions. The lateral wall of the myodome is formed by the prootic and parasphenoid; the medial wall is formed by the prootic. The posterior termination of the myodome lies at about the midpoint between the anterior border of the lateral parasphenoid wing and the posterior border of the parasphenoid.

Otic and Occipital Regions and Posttemporal Fossa

The supraoccipital is a single median bone lying at the dorsoposterior apex of the skull (Figs. 3–7). From posterior view, the bone is roughly triangular, with a ventral apex; it has synchondral articulations with the epioccipitals along its posterolateral borders. Dorsally, the supraoccipital is very broadly convex, with about half of its area overlain by the parietals. There is a very small supraoccipital crest.

The medial surface of the supraoccipital forms the internal posterodorsal roof of the cranial fossa. There is a perichondrally lightly ossified area which curves around the dorsal portion of the posterior vertical semicircular canal.

The epioccipitals (=epiotics, *sensu lato*; see Patterson, 1975: 425) are paired, perichondral ossifications that form the dorsoposterior part of the braincase and contain the posterior vertical semicircular canals (Figs. 3, 4, 6, 7). The epioccipital has synchondral joints with the supraoccipital medially, the pterotic laterally, and the exoccipital ventrally. The posteroventral surface of the intercalar articulates syndesmotically with the epioccipital.

The medial surface of the epioccipital consists primarily of a perichondrally ossified canal through which passes the posterior vertical semicircular canal (Fig. 5).

The exoccipitals are paired bones which form the largest portion of the posterior of the skull (Figs. 3–7). There are synchondral joints with the epioccipitals dorsally, the pterotic anterodorsally, the contralateral exoccipital medially, the prootic anterolaterally, and the basioccipital ventrally. The intercalar overlies the posterodorsal and dorsolateral exoccipital surfaces and articulates in a thick syndesmotic joint. The anterior border of the exoccipital, adjacent to the prootic, is nearly vertical to the longitudinal body axis; the ventral border, adjacent to the basioccipital, is nearly horizontal. The dorsal border extends laterally and ventrally at the posterolateral corner of the neurocranium, then is broadly convex along the posterior region of the skull. The posteromedial border is vertical dorsally, then deeply concave where it forms

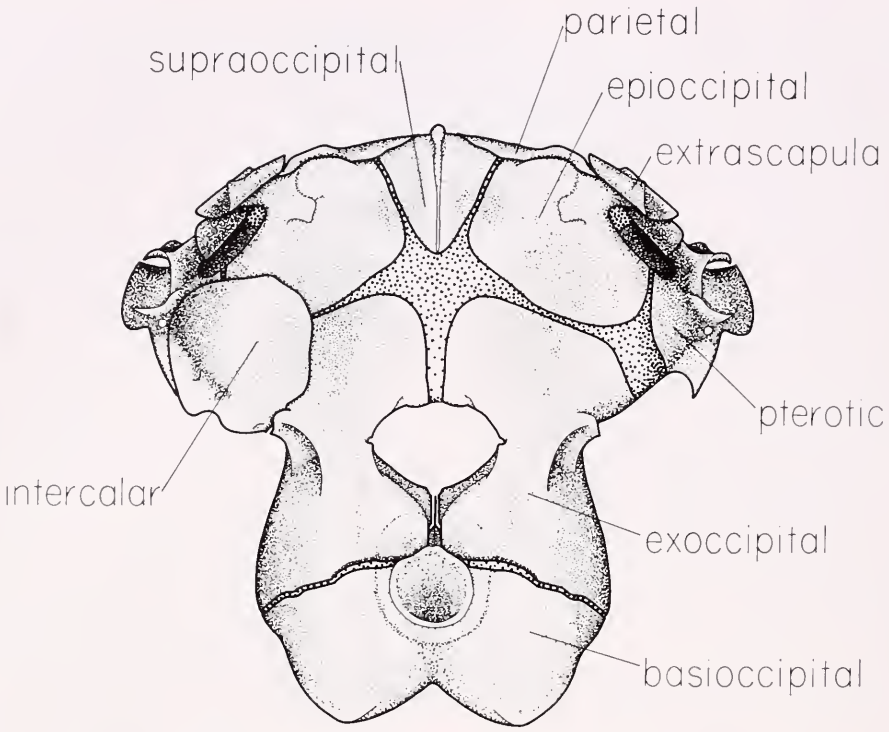

Figure 7. Neurocranium of *D. taenia* (USNM 206614; 171.0 mm SL), posterior view.

the border of the foramen magnum, excluding the basioccipital from the foramen magnum. Ventral to the foramen magnum, the exoccipital bears a wide articular facet which forms, with the basioccipital (see below), a deeply concave articular surface for the notochord. The foramen for the ninth and tenth cranial nerves is a prominent feature of the exoccipital (Fig. 7).

The medial surface of the exoccipital forms the posterolateral and posterodorsal walls of a deep cavity which contains the saccular and lagenar portions of the ear. In addition, there is a deep concavity dorsolaterally on the exoccipital in which lies the ampulla at the junction of the posterior portions of the horizontal and posterior vertical semicircular canals.

The basioccipital is a single bone which forms the posterior floor of the neurocranium (Figs. 4–7). Anteriorly, the basioccipital extends to a point about midway between the posterior surface of the neurocranium and the anteroventral border of the prootic. Anteroventrally the basioccipital lies dorsal to the parasphenoid, which is tightly joined to it syndesmotically and synchondrally. The broadly concave anterior border of the basioccipital has a synchondral joint with the prootic; the nearly straight dorsal border has a synchondral joint with the exoccipital. Posteriorly the basioccipital has a deeply concave articular surface for the notochord. The basioccipital forms the floor of the lagenar capsule.

The shape of the basioccipital in medial view is illustrated in Figures 5 and 6. There are bilateral, very deep concavities in the bone in which lie the saccular and lagenar portions of the ear. The large medial flange of bone separating the two concavities is visible in Figure 7 just ven-

tral to the foramen magnum and medial to the posteromedial borders of the exoccipitals.

The intercalars are paired dermal bones which overlay and have tight syndesmotic joints with the epioccipitals, pterotics, and exoccipitals (Figs. 3, 7). The posterolateral apex of the intercalar is a process which serves as the attachment site for the ligament extending from the anteroventral ramus of the posttemporal.

The prootics are paired bones which form much of the lateral walls of the braincase (Figs. 4–6). Ventrally, the prootic lies medial to, and has a broad syndesmotic articulation with, the parasphenoid. The prootic has synchondral articulations with the basisphenoid anteroventrally, the pterosphenoid anterodorsally, the sphenotic anterolaterally, the pterotic posterolaterally, the exoccipital posteriorly, and the basioccipital posteroventrally. The lateral external face of the prootic is more or less concave as it extends dorsolaterally from its ventral articulation with the parasphenoid to its articulation with the sphenotic and pterosphenoid. The prootic contains foramina for the complex of the fifth and seventh cranial nerves.

In medial view the prootic shape is complex (Figs. 5, 6). Ventrally, there is a broad medial extension which articulates synchondrally with the contralateral prootic; this broad extension forms the roof of the posterior myodome. Posteromedially, there is a broad, deep concavity in which lies the anterior of the sacculus and its large otolith (saggita). Dorsolaterally, there is a broad concavity in which lies the utriculus.

The pterotics are paired compound bones which lie on the posterolateral border of the skull (Figs. 3, 4, 6, 7). There are synchondral articulations with the prootic anteroventrally. On the dorsal surface of the skull, the pterotic has an anterior ramus which partially overlies the sphenotic; the medial border is convex and broadly overlies the parietal (fitting into a shallow concavity on the dorsal surface of that bone). The dorsal anterior ramus is itself overlain by the dermosphenotic. A laterosensory canal extends along the dorsolateral pterotic surface and is partially enclosed by bone. The ventrolateral surface of the pterotic bears a long groove, the hyomandibular fossa. The ventral surface of the pterotic is concave.

The medial surface of the pterotic, which partially lines the cranial fossa, is primarily an ossification which contains the horizontal semicircular canal (Figs. 5, 6).

The posttemporal fossa lies in the posterior region of the neurocranium, near its dorsolateral border. The opening of the fossa is bordered medially by the epioccipital, and laterally by the pterotic. The dorsal wall and part of the medial wall of the fossa are formed by the parietal, the vertical and lateral walls by the pterotic. The fossa extends anteriorly to a point at about the mid-length of the pterotic, as viewed from dorsal aspect.

Circumorbital Bones

The orbital bone series of *Diplophos* is well developed and heavily ossified (Fig. 8).

The supraorbital is a thin elongate bone which forms the anterodorsal border of the orbit. The bone lies lateral to the frontal and posterolateral to the olfactory fossa. The anteromedial border of the supraorbital forms a small portion of the border of the olfactory fossa. The dorsal surface of the supraorbital is concave as the bone spreads laterally out over the eye.

The antorbital is a wafer-like thin bone which lies anterior to the orbit; its dorsoposterior border usually forms the lateral border of the olfactory capsule. In some specimens, the antorbital slightly overlies the maxilla. The antorbital may lie somewhat anteriorly offset from the

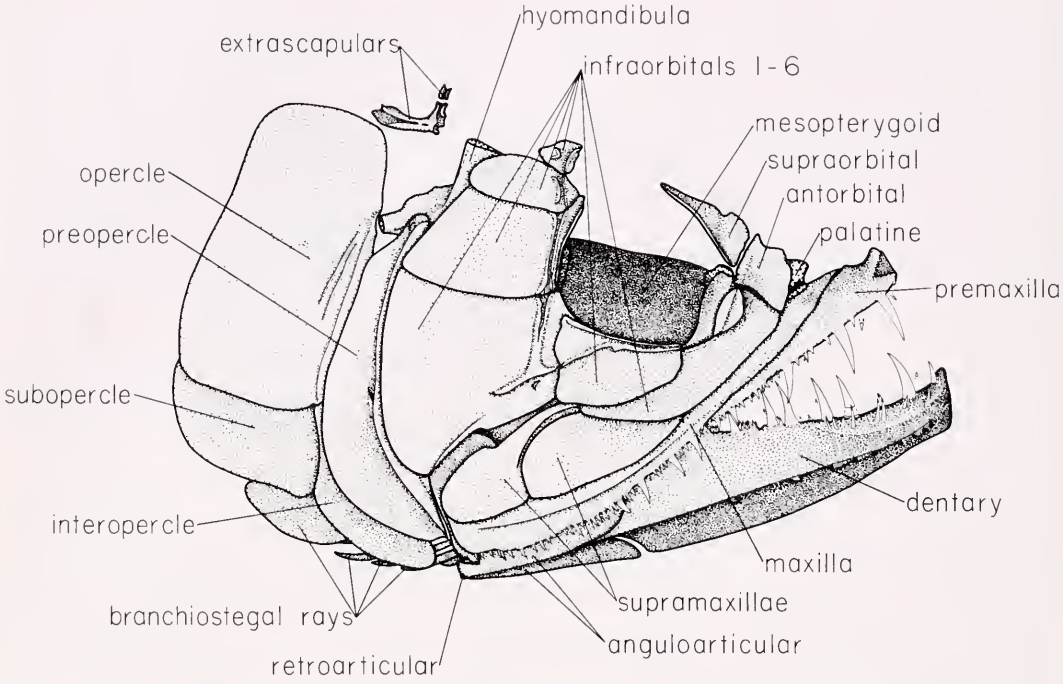

Figure 8. Suspensorium and infraorbital bone series of *D. taenia* (USNM 206614; 171.0 mm SL), lateral view.

supraorbital and the first infraorbital (IO1), so may be excluded from the anterior border of the orbit.

Infraorbital 1 lies along the anteroventral border of the orbit. There is a small sensory canal on the dorsal border, anteriorly. Anteriorly, the dorsal border is concave and follows the rim of the orbit; more posteriorly, the dorsal border becomes gently convex. The ventral border is more or less convex. Posteriorly, IO1 lies medial to IO2.

Infraorbital 2 forms the ventral border of the orbit. There is a laterally-projecting bony lamella along the dorsal border of IO2. Anteriorly, an open sensory canal extends just ventral to the lamella, then, just posterior to the mid-length of the bone, the canal extends posteroventrally to meet the canal on IO3. The ventral border of the thin bony lamella of IO2 is more or less convex. The posterior border of IO2 is slightly convex dorsally, between the dorsal border of the bone and the sensory canal; ventral to the sensory canal, the border may be more or less posterior to IO1 and the anterior portion of IO3.

Infraorbital 3 is the largest of the infraorbital series. Anterodorsally, its border forms a portion of the orbital rim; posteriorly, the bone covers much of the "cheek" area and the adductor mandibulae muscles. The ventral border of IO3 is slightly convex anteriorly; more posteriorly, there is an abrupt ventral angle, and the ventral border is more deeply concave (this is dorsal to the area where the supramaxilla abuts IO3). The posterior border of IO3 is broadly convex and is tightly bound to the preopercle. The dorsal border of IO3 underlies IO4 and is gently concave. There is a sensory canal on IO3 which may be open or partially open and which consists of a vertical canal, an anterior canal, and one or two small, short, posterior canals.

Infraorbital 4 lies posterior to the orbit,

forming part of its posterior border. Anteriorly, IO4 has a well-developed sensory canal, nearly enclosed, which angles dorsally and slightly posteriorly, and is contiguous with the canal on IO5. The anterior border has a laterally-projecting flange, which is anterior to the sensory canal. The anterior and dorsal borders of IO4 are slightly concave; the ventral and posterior borders are slightly convex. The dorsal border lies medial to IO5, and the ventral border lies lateral to IO3.

Infraorbital 5 is smaller than IO4; it is more or less oblong in shape. The bone is excluded from the orbit by IO4. A small, open sensory canal lies in the anterior region of the infraorbital. The ventral border lies lateral to IO4; a small segment of the dorsal border is medial to IO6.

Infraorbital 6 (dermosphenotic) is a small bone which lies dorsal to IO5. The bone articulates syndesmotically on the flat anterior surface of the pterotic and on the posterior surface of the sphenotic. In specimens of *D. taenia*, IO6 is a rather short bone in an anteroposterior axis, being bluntly triangular or oblong. In *D. maderensis*, IO6 is a more elongate bone, extending more posteriorly on the pterotic. In both species there is an open sensory canal in the anterior region of the bone.

Nasals

The nasals are paired bones which lie medial to and partially form the medial borders of the olfactory fossae (Fig. 2). The nasal is syndesmotically articulated with the dorsal surface of the rostrodermethmoid. The nasal is primarily an open bony canal which arches around the olfactory fossa.

Upper Jaw

The premaxillae are paired, toothed bones which form the anterodorsal border of the mouth (Figs. 4, 8). There is a small articular process anteriorly. The premaxilla is slightly curved from dorsal aspect, is relatively broad anteriorly, and tapers to a blunt point posteriorly. Posterior to the articular process there is a deep concave facet, which serves as the articulation point with the maxilla. At the symphysis there is a slight concavity on the anterior surface of the premaxilla. On the posterior surface near the symphysis there is a concavity which serves as an attachment site for suspensory ligaments (see page 56). There are about five to eight fang-like teeth and numerous smaller teeth ankylosed to the ventral border of the bone (Type 1 of Fink, 1981).

The maxillae are paired bones which form the posterodorsal border of the mouth (Figs. 4, 8). Each maxilla is an elongate bone which is, from dorsal aspect, somewhat broad anteriorly and slender posteriorly. The medial surface of the anterior border of the maxilla is extended as a condyle. Ventral to the condyle is a convexity on which the anterior premaxillary-maxillary ligament attaches (Fig. 13). Anterolaterally near the symphysis, there is a shallow facet which articulates in the concavity on the posterior surface of the articular process of the premaxilla. For about half its length the maxilla articulates with the dorsomedial surface of the premaxilla and is toothless. At about the mid-length of the maxilla, the ventral border of the bone angles ventralward and becomes slightly convex to its posterior termination; in this area the ventral border bears numerous teeth (Fig. 8). The more anterior teeth are larger than those more posterior; all mature teeth have Type 1 attachment mode. The toothed area of the maxilla anteriorly meets the posterior extension of the premaxilla; thus, the upper border of the mouth is toothed along its entire length. At about the middle of the lateral surface along the tooth-bearing portion of the maxilla there is a small lateral lamella of bone (Fig. 8).

There are two pairs of supramaxillary bones. The anterior supramaxilla lies in

connective tissue dorsal to the anterior toothed portion of the maxilla and articulates with the dorsolateral surface of that bone (Fig. 8). The ventral border of the anterior supramaxilla is nearly straight or slightly convex. Anteriorly, the bone border is broadly convex. The dorsal border is slightly concave anteriorly and broadly convex posteriorly. The posterior border is broadly convex. The bone, in a dorsoventral plane, is much larger posteriorly than anteriorly. The dorsal and posterior borders lie lateral to, and attach by dense connective tissue to, the posterior supramaxilla.

The posterior supramaxilla is an elongate, thin bone that lies medial and posterior to the anterior supramaxilla and dorsal to the posterior area of the tooth-bearing portion of the maxilla (Fig. 8). Posteriorly, the ventral border of the posterior supramaxilla is more or less straight and in line with the same border of the anterior supramaxilla, articulating with the dorsolateral face of the maxilla. Anteriorly, the ventral border is deeply concave, roughly matching the curvature of the posterodorsal border of the anterior supramaxilla. The dorsal border of the posterior supramaxilla is convex anteriorly, then concave for a short distance, then posteriorly is convex to the posterior termination of the bone. Thus, the posterior supramaxilla has two portions: an anterior slender, curving ramus of bone and a more oblong posterior section. The anterior ramus bears a lateral facet into which articulates the posterodorsal border of the anterior supramaxilla (Fig. 8).

Lower Jaw

The dentaries are paired and are the tooth-bearing bones which form most of the ventral border of the mouth (Figs. 4, 8). From dorsal aspect, the main body of the dentary is more or less straight posteriorly, arching medially anteriorly. The dentaries are joined at the midline anteriorly by a strong syndesmotic joint. The main body of the dentary contains a deep median fossa for attachment of the adductor muscles (Fig. 4). Ventral to this main dentary body is a long bony flange which forms the ventral border for most of the dentary length.

The dorsal border of the dentary bears four to eight large fang-like teeth and numerous smaller teeth. Anteriorly there is a short outer row of five to nine slender teeth and an inner row of much larger caniniform teeth. Posteriorly the teeth are all more or less in a single row; here the small teeth are much smaller than the large caniniform teeth. All teeth have Type 1 attachment mode. The posteromedial border of the dentary is deeply concave and is the medial border of the mandibular fossa; the posterolateral border of the dentary is also concave, but the concavity extends anteriorly less than half the distance of the medial border.

The anguloarticulars are paired bones which form the major posterior portion of the mandible (Figs. 4, 8). The bone is of complex shape. Anteriorly the bone lies medial and dorsal to the lateral and ventral walls of the mandibular fossa of the dentary. The ventral border of the anguloarticular extends anteriorly to a point just anterior to the medial border of the fossa on the dentary; in the region dorsal to the ventral flange of the dentary, the ventral border of the anguloarticular is straight, but posterior to that area the anguloarticular has its own ventral flange (Fig. 8). The dorsal anguloarticular border is concave anteriorly (Fig. 8) and slightly convex posteriorly. The posterior border is deeply convex dorsally and deeply concave ventrally, where there is an articular facet for the quadrate. The inner wall of the anguloarticular forms a shallow fossa, continuous with that of the dentary; posteriorly there is a medial wall of the fossa.

The retroarticular is a small cap of bone which articulates tightly against the posteromedial apex of the anguloarticular (Figs. 4, 8).

Meckel's cartilage is a slender rod of cartilage which extends along the floor of the mandibular fossa from a small condyle on the anguloarticular at the ventral border of the inner wall of the fossa (Fig. 4) to near the symphysis in the main body of the dentary.

Palatine Arch and Dorsal Portion of the Hyoid Arch

The quadrates are paired bones that form the ventral portions of the suspensoria, to which the mandible articulates (Fig. 4). The quadrate is more or less triangular, with a ventral apex in the form of an articular facet for the anguloarticular. The anterior border of the quadrate is more or less straight and extends in an anterodorsal direction. The anterior border lies lateral to and articulates by connective tissue with the posterior border of the ectopterygoid. The dorsal border of the quadrate is slightly convex and has a synchondral joint with the metapterygoid bone. The posterior border of the quadrate proper is more or less straight and is nearly vertical or canted slightly dorsoposteriorly. The posterior quadrate border has a tight syndesmotic joint with the symplectic, which lies against it. Posterolateral to the posterior quadrate border is a slender bony flange which has a slightly convex border, and which extends from near the dorsalmost point of the quadrate to near the articular facet.

The ectopterygoid bones form the posteroventral borders of the palatine arches (Fig. 4). The ectopterygoid is an elongate bone which extends from near the articulation of the quadrate and the anguloarticular to a point near the anterior articulations of the palatine with the neurocranium. The ventral border of the ectopterygoid is very broadly concave. The anterior border has a tight syndesmotic joint with the posterodorsal surface of the palatine bone and is tapered anterodorsally to a blunt point. The dorsal border of the ectopterygoid is more or less straight or slightly concave. The posterior border is somewhat variable among individuals and may be slightly convex ventrally and rather deeply concave dorsally, or it may be slightly concave, with a convexity near the dorsal border (Fig. 4). Along the dorsal border of the ectopterygoid there are two bony flanges, one which extends anterolaterally and one which extends medially along the entire dorsal border of the bone. Within the concavity formed by these flanges is the articular surface for the synchondral joints with the mesopterygoid anteriorly and the metapterygoid posteriorly. The anterolateral flange of the ectopterygoid lies lateral to the mesopterygoid articulation and ventral to the metapterygoid articulation. The medial flange of bone lies medial or ventromedial to the mesopterygoid and medial to the metapterygoid (Fig. 4).

The palatine bones form the anteroventral borders of the palatine arch (Figs. 4, 13, 14). The palatine can be seen to consist of two condyles which articulate with the neurocranium and a posterior ramus which extends ventral to the ectopterygoid. The anterior condyle articulates with the ethmoid cartilage in the area of the prenasal process. This condyle is more or less triangular in cross section and has a large cartilaginous tip. The ventral border has a small edge which has one to four recurved teeth; this toothed ridge is slightly medial to the tooth-bearing portion of the posterior palatine ramus. The posterior condyle lies posteromedial to the anterior condyle and articulates with the ethmoid cartilage in the region of the lateral ethmoid (Fig. 4). This condyle is quite broad and has a concave dorsal surface. The medial bony border is deeply convex from dorsal aspect; the medial cartilaginous border extends medially to near the anteromedial border of the mesopterygoid in small specimens and forms a synchondral joint with that bone in large specimens. Posteriorly, the posterior condyle overlaps

the mesopterygoid, which articulates in a shallow facet on the ventral palatine surface. The posterior palatine ramus extends posteriorly about one-quarter the anterior length of the ectopterygoid; the ramus tapers to a blunt point near the ventral border of the ectopterygoid. The ventrolateral border of the palatine bears a row of small recurved teeth; the anterior teeth are larger than those more posterior.

The mesopterygoids are paired bones which form the largest part of the dorsal wall of the palatine arch (Fig. 4). The dorsal two-thirds of the bone forms a concave "cup" which forms the medial wall of the orbit. The anterodorsal border of the bone is more or less straight or slightly convex anteriorly. The anterior ventral border is slightly concave at the articulation point with the palatine in the region of its condyle. The joint with the palatine is syndesmotic. The anterior border of the mesopterygoid lies ventromedial to the palatine condyle; in some specimens there is an anterior extension of the mesopterygoid which articulates in a facet on the ventral surface of the palatine condyle. The ventral border of the mesopterygoid tightly articulates with the ectopterygoid, as described above; the ventral border of the mesopterygoid lies lateral to the border of the ectopterygoid. The posterior border of the mesopterygoid is concave dorsally, and near its midpoint there is a posterior extension which extends under the medial surface of the metapterygoid; ventral to this extension, the posterior border may be slightly concave or slightly convex; the posterior mesopterygoid border is tightly articulated with the anterior of the metapterygoid. At the medialmost part of the mesopterygoid, ventral to the orbit, is a patch of numerous small teeth.

The metapterygoid bones are paired and form the posterodorsal wall of the palatine arch (Fig. 4). The anteroventral border is broadly convex, articulating synchondrally with the quadrate posteroventrally and the ectopterygoid anteroventrally, and syndesmotically with the ectopterygoid anteriorly. There is a small anterodorsal ramus of the metapterygoid that extends somewhat lateral to the main vertical axis of the bone; this ramus is continuous with a bony flange that extends somewhat medially as the dorsal and posterior borders of the mesopterygoid bone. At about the midpoint of the dorsal border there is a large dorsolaterally-projecting flange that reaches an apex as the posterodorsalmost point of the bone. The flange is continuous along the posterior border of the bone to its posteroventral apex. The medial flange articulates synchondrally with the anteromedial surface of the ventral body of the hyomandibula; the lateral flange articulates with or lies lateral to the lateral border of the ventral body of the hyomandibula. In *D. taenia* the dorsal border of the metapterygoid, represented by the medial flange, lies near or articulates synchondrally with the anterodorsal flange of the hyomandibula and is more or less straight or slightly convex posteriorly; there is a rather marked angle at the junction of the dorsal and posterior borders. In *D. maderensis*, the metapterygoid dorsal border lies ventral to the hyomandibular flange, and the dorsal border is convex and continuous with the posterior metapterygoid border.

The hyomandibulae are paired bones which serve to brace the palatine arch to the neurocranium posteriorly, and which also articulate with much of the opercular series (Fig. 4). The hyomandibula is broadest in the anteroposterior plane near its dorsal border. The main body of the bone, which is endochondral, becomes abruptly narrower ventrally, forming a single elongate ventral ramus which extends to a point near the ventral border of the metapterygoid bone. There is a large anterior bony flange on the hyomandibula for about half its length; for a description of the flange shape and relationships with the metapterygoid, see the

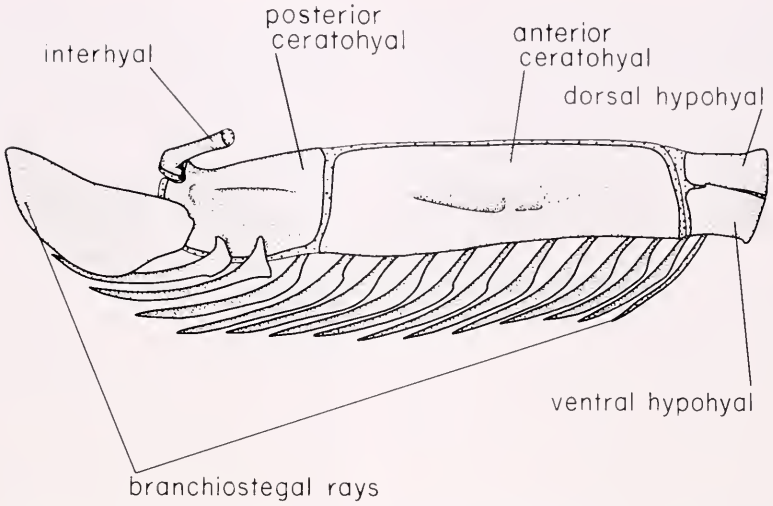

Figure 9. Hyoid arch, ventral portion, of *D. taenia* (USNM 206614; 171.0 mm SL).

description of that bone, above. On the posterior border of the hyomandibula there is a laterally-projecting bony flange which extends from near the dorsal border of the bone to near the ventral border at the apex of the elongate ventral ramus. At about one-third the distance from the dorsal border along the hyomandibula there is a large posteroventrally directed cartilage-tipped condyle for the diarthrodial articulation of the opercle. Small bony flanges extend from the dorsal and ventral borders of the condyle to the posteromedial hyomandibular border.

A small photophore lies in the integument near the ventrolateral surface of the articular condyle. The dorsal border of the hyomandibula articulates in a diarthrodial joint with the neurocranium in the hyomandibular fossa on the ventral surfaces of the sphenotic and pterotic bones. The anterior border of the hyomandibula articulates with the metapterygoid as described above under the latter bone. The ventral border articulates diarthrodially with the symplectic, the interhyal, and the posterodorsal border of the quadrate; in some specimens there may be a small diarthrodial articulation with the metapterygoid. The posterior hyomandibular border articulates syndesmotically along most of its border with the anterior border of the preopercle.

The symplectic is a slender bone which articulates syndesmotically tightly against the posteromedial surface of the quadrate (Fig. 4). The bone is shaped like an elongate cone, with its small apex ventrally, and with its somewhat expanded dorsal border capped by a large bulbous cartilage body. The dorsal cartilage articulates anteriorly with the quadrate and metapterygoid, dorsally with the hyomandibular, and posteriorly with the interhyal.

Ventral Portion of the Hyoid Arch

The interhyal is a rod-shaped bone which connects the ventral portion of the hyoid arch to the suspensorium (Figs. 4, 9). Dorsally there is a dome-shaped cartilage which articulates diarthrodially with the symplectic and hyomandibula. Ventrally the interhyal has a wide, cartilage-lined facet which articulates diarthrodially with the posterior ceratohyal bone.

The posterior ceratohyal forms about 20–25% of the length of the hyoid bar (Fig. 9). It is thin in cross section. In lateral view, the dorsal border is concave

posteriorly and straight anteriorly. The posterior border is composed primarily of the articular facet for the interhyal and consists of a deep cartilage-lined dorsal concavity; ventral to the articular surface the border is deeply convex and is continuous with the long convex ventral border. The anterior border is also broadly convex and diarthrodially articulates with the anterior ceratohyal. Four branchiostegal rays attach to the posterior ceratohyal; the posterior three articulate on the ventrolateral surface of the bone, the anterior ray on the medial surface very near the anterior ossified border of the bone.

The anterior ceratohyal is an elongate bone, also thin in cross section, which makes up the bulk of the hyoid bar (Fig. 9). In lateral view, its dorsal border is more or less straight or slightly convex; the posterior border is slightly convex and articulates synchondrally with the posterior ceratohyal; the anterior border is also slightly convex, and there is a large cartilage extension beyond the ossification which articulates diarthrodially with the dorsal and ventral hypohyals; the ventral border is slightly concave. Eight branchiostegal rays articulate with the ventromedial surface of the anterior ceratohyal in *D. maderensis*, nine in *D. taenia*.

The dorsal and ventral hypohyals are ossifications of a single cartilage block which lies anterior to the anterior ceratohyal (Figs. 9, 10). The dorsal hypohyal is slightly concave dorsally; anterodorsally, there is an articular facet for the basihyal and for a ligament to the first gill arch; the anterior border of the bone ventral to the articular facet is straight. The ventral border is more or less straight, becoming convex posteriorly; this convexity is continuous with the slightly convex posterior border of the bone. Ventral to the ventral border of the dorsal hypohyal is a cartilaginous area; ventral to that area is the straight or slightly convex dorsal border of the ventral hypohyal (in large specimens the cartilaginous area is so small that there is a tight synchondral joint between the bones). The posterior border of the ventral hypohyal is straight or slightly concave; the ventral border is slightly concave; the anterior border is more or less straight. In the medial surfaces of both hypohyals is a continuous deep concavity which lies in a dorsoventral plane; this concavity is the articulation point for the basibranchial of the first gill arch. One branchiostegal articulates with the posteromedial surface of the ventral hypohyal in *D. maderensis*, two in *D. taenia*.

The basihyal articulates with the anterodorsal and anterior borders of the basibranchial of the first gill arch, medial to the dorsal and ventral hypohyals (Fig. 10). Anteriorly the basihyal consists of a large rounded dome of cartilage with a dorsal perichondral ossification. The ossification extends posteriorly along the dorsal surface of the basibranchial and is somewhat wider laterally than the anterior ossified portion. There is a small tooth patch of small recurved teeth on the dorsal surface of the posterior bony portion of the basihyal. Basihyal morphology in *Diplophos* was illustrated by Weitzman (1974, Fig. 75B).

The urohyal is a single elongate median bone which lies ventral to the gill arches. The anterior portion of the urohyal is a well-developed condylar area which forms the anterodorsal apex of the bone. In large specimens this area is joined to the rest of the urohyal by a slender "neck." Anterodorsally on this condylar portion there are short bilateral rami which serve as attachment sites for ligaments extending to the anterior borders of the ventral hypohyals; anteroventrally, there is an attachment site for a ligament extending to the anteroventral border of the ventral hypohyal. Posterior to the articular condyles, the dorsal urohyal border is very broadly convex. In large specimens the dorsal border is represented by a median flange of bone

which extends beyond the more heavily ossified body of the bone. In smaller specimens, the anterior border extends ventrally from the articular condylar area as a more or less straight line which then becomes convex and continuous with the broadly convex, slightly irregular, ventral border; in larger specimens the anterior border is convex and continuous with the ventral border. The ventral border meets the dorsal border at the dorsoposterior apex of the bone. The urohyal is, for most of its area, a very thin plate of bone; both the anterior and dorsal urohyal borders are more heavily ossified than the rest of the urohyal except for the anterodorsal condylar area.

Opercular Bones

The preopercle is the anterior bone in the series (Figs. 4, 8). In *D. maderensis* examined, the main body of the preopercle is an enclosed bony sensory canal which has a more or less dorsoventral main axis; ventrally, this bone angles anteroventrally. The anterior preopercular border is more or less straight dorsally; in the region of the posteroventral border of the metapterygoid, the preopercular border is composed of a bony flange which curves slightly concavely and articulates syndesmotically against the posterior border of the quadrate. Extending from the posterior border of the enclosed canal are two flanges, one posterior and one posterolateral; both flanges have their dorsal borders near the posteroventral border of the dorsal opening of the canal. Dorsally, the posterior flange is more or less straight or slightly concave; ventrally, the border is broadly convex. The posterolateral flange is smaller than the posterior flange and is slightly convex dorsally and broadly convex ventrally. The preopercular canal has its ventral opening at about the midpoint of the broadly convex area of the posterolateral flange.

The preopercle in *D. taenia* specimens examined (all of which are larger than the *D. maderensis* examined) has no fully enclosed bony canal. The posterior and posterolateral flanges extend as in *D. maderensis* but are not interconnected by a posterior bony wall. There may be a small connection between the two flanges at about the mid-length of the preopercle (see Fig. 8).

In all specimens examined, the posterior borders of infraorbitals 3 and 4 articulate lateral to the posterolateral preopercular flange. The posteromedial border of the posterior flange articulates tightly against the opercle.

The opercle is the largest bone in the opercular series (Figs. 4, 8). The bone has a slightly convex dorsal border. The anterior border is somewhat concave dorsal to the articulation with the hyomandibula, and somewhat convex ventral to that point. The articular facet lies at a distance from the dorsal border of about 20–25% of the dorsoventral length of the bone. On the medial opercular surface, a ridge of bone extends posteroventrally from the articular surface; a second ridge follows the anterior border of the opercle. On the lateral surface of the opercle there is a small bony flange extending laterally, just posterior to the anterior border of the bone; this flange articulates against the posterior border of the preopercle. The ventral opercular border is slightly convex or more or less straight. The posterior opercular border is slightly convex dorsally and ventrally, with a concave area between the convexities.

The subopercle lies ventral and medial to the opercle (Figs. 4, 8). The bone is somewhat rectangular in shape, and about equal in anteroposterior length to the opercle. The anterodorsal corner is a small area of reinforced bone; from that area, the anterior border is somewhat S-shaped, concave dorsally and convex ventrally. The ventral border is more or less straight anteriorly, broadly convex posteriorly and continuous with the posterior border. The dorsal border is some-

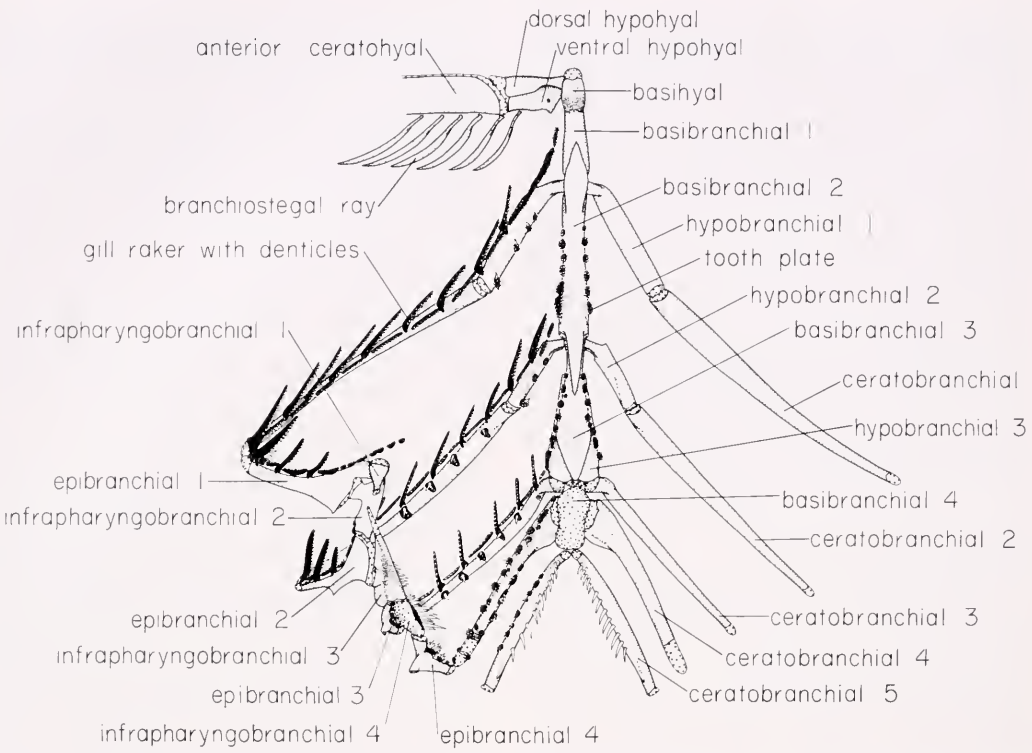

Figure 10. Branchial apparatus of *D. taenia* (USNM 206614; 171.0 mm SL), dorsal view; portions of right side removed; left side spread laterally. Tooth plates in black.

what concave anteriorly and straight posteriorly. About 20% of the dorsal area of the subopercle lies medial to the opercle. The anterior border lies medial to and articulates with the interopercle.

The interopercle is an irregularly-shaped bone which lies anterior and anteroventral to the subopercle (Figs. 4, 8). Ventrally, the anterior border is slightly concave, with an indentation in the area near the interhyal bone; dorsally, the anterior border is convex. The posterior border is convex along its articulation with the subopercle and then broadly convex to the anteroventral apex of the bone. The interopercle articulates by connective tissue to the medial surface of the preopercle (see Fig. 4).

Branchial Apparatus

The infrapharyngobranchial of the first arch is a rod-shaped bone which is relatively thin in cross section dorsally, and larger and almost triangular in cross section ventrally. It articulates dorsally with the prootic, near the midpoint of that bone (Fig. 4), and ventrally diarthrodially with the anterolateral border of the epibranchial of the first arch (Figs. 10, 11). There are no tooth plates associated with infrapharyngobranchial 1. The bone lies, in lateral view, in a more or less dorsoventral plane and suspends the gill apparatus from the neurocranium.

Infrapharyngobranchial 2 is a bone nearly twice the length of infrapharyn-

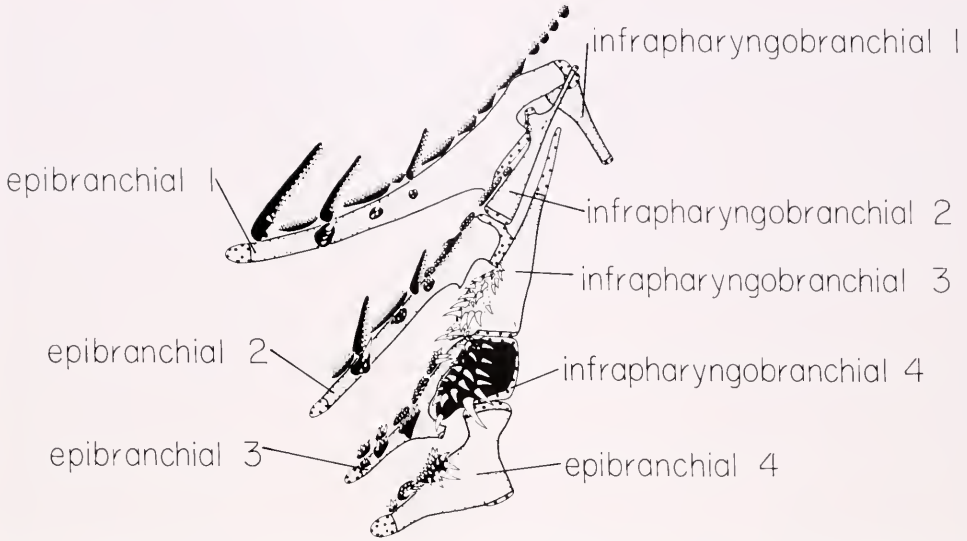

Figure 11. Dorsal portion of branchial apparatus of *D. taenia* (USNM 206614; 171.0 mm SL). Tooth plates in black.

gobranchial 1 (Figs. 10, 11). It consists of a long slender, anteriorly projecting ramus, cartilage-capped, which reaches a point equal to the anterior extent of epibranchial 1 and articulates diarthrodially with that bone. Posterior to the elongate anterior ramus is a vertical ramus which forms an uncinate process; it, too, is cartilage-capped, and it articulates with a concavity in the anterodorsal surface of epibranchial 1. Posteriorly, infrapharyngobranchial 2 is broader and articulates diarthrodially with epibranchial 2. There is an elongate tooth patch along the posterolateral border of the second infrapharyngobranchial. The *in vivo* alignment of the bone is anteromedial to posterolateral. There is a slender bony flange, convex from dorsal aspect, which extends along the medial border of the bone from the anterior portion of the anterior ramus to the posteromedial border of the bone near its articulation with the epibranchial.

Infrapharyngobranchial 3 is somewhat longer than infrapharyngobranchial 2 and lies posterior and medial to that bone (Figs. 10, 11). There is an elongate anterior ramus whose ossification border is near the level of the dorsal uncinate process of infrapharyngobranchial 2 and which extends, as cartilage, to articulate near the anteromedial border of infrapharyngobranchial 2. At about the midlength of the bone, there is a large concave articular facet laterally, in which the epibranchial of the second arch tightly articulates diarthrodially. Posterior to that point, the bone becomes much wider, carrying on its ventrolateral surface a large bony tooth plate with numerous Type 3 teeth (Fink, 1981). The tooth plate is fused to the infrapharyngobranchial and extends posterolaterally somewhat beyond the border of the infrapharyngobranchial proper. The teeth are fairly large, much larger than those on the small tooth plate associated with infrapharyngobranchial 2. The posterior border of infrapharyngobranchial 3 is more or less straight or slightly convex and articulates diarthrodially with infrapharyngobranchial 4 for most of its width and laterally with the dorsal extension of the

epibranchial from the third gill arch. There is a wide bony flange extending from near the anterior ossification border of the anterior ramus, medially to near the posteromedial border of the infrapharyngobranchial.

Infrapharyngobranchial 4 is an almost cube-shaped cartilaginous body which diarthrodially articulates anteriorly with infrapharyngobranchial 3 and posteriorly with the epibranchial of the fourth arch (Figs. 10, 11). There is a large toothplate tightly bound to the ventral surface of infrapharyngobranchial 4; part of the ossification of this toothplate overlaps the lateral border of the cartilage and extends onto its dorsal surface; otherwise, the dorsal surface of the infrapharyngobranchial is unossified. The toothplate extends posterolaterally somewhat beyond the cartilage border. The teeth are Type 3.

The epibranchial of the first arch is an elongate bone (Figs. 10, 11). Anteriorly, it has an anterior-extending ramus, more or less round in cross section, which articulates with infrapharyngobranchial 1, as described above. Somewhat posterior to that region, there is an expanded dorsal condyle, capped with cartilage, followed posteriorly by a bony flange with a concave border. Anterior to the condyle is a deep concavity which extends forward to the base of the anterior extension of the anterior ramus. The dorsal uncinate process of infrapharyngobranchial 2 articulates in this concavity. Posteriorly, epibranchial 1 articulates diarthrodially with ceratobranchial 1. Along the anterior border of epibranchial 1 lie several small bony tooth plates (with Type 1 teeth) that extend from the skin of the roof of the mouth down onto the skin over the bone. There are three, anteriorly projecting, toothed gill rakers; in each space between the rakers lies an elongate, bony tooth plate with numerous small teeth.

Epibranchial 2 is quite broad anteriorly, in a dorsoventral plane (Figs. 10, 11). The anterior region of the bone is a very large, complex cartilaginous surface which articulates anteriorly with infrapharyngobranchial 2 and medially with infrapharyngobranchial 3. There is a small dorsal flange of bone anteriorly. Posteriorly, the bone articulates with ceratobranchial 2. There are two or three gill rakers on the anterior border and elongate tooth plates between them.

Epibranchial 3 is much less broad anteriorly than epibranchial 2; there is a medially-curved anterior process which articulates diarthrodially between infrapharyngobranchials 3 and 4 (Figs. 10, 11). About midway along the length of the bone there is a dorsally-directed process, cartilage-capped, and a flange of bone ventral to that. Posteriorly, the epibranchial articulates diarthrodially with ceratobranchial 3. Epibranchial 3 has a toothplate medially, and about five or six smaller toothplates along its medial border.

Epibranchial 4 is quite large, very broad anteriorly, articulating diarthrodially across a broad cartilaginous joint with infrapharyngobranchial 4 (Figs. 10, 11). On the dorsal surface of the bone, at about its mid-length, there is a very large cartilage-tipped articular condyle, and posterior to that a large thin flange of bone that extends almost to the ventral border of the bone, where the bone articulates with ceratobranchial 4. There is a large, well-developed tooth plate on the ventral surface of epibranchial 4, at about its mid-length, and ventral to that another, smaller toothplate in the skin; lateral to that toothplate is another, much smaller.

The ceratobranchials are all much alike and will be described only briefly. The ceratobranchials form the major portion of the ventral part of the gill apparatus, articulating dorsally with the epibranchials and articulating ventrally with the hypobranchials (Fig. 10), excepting those of the fourth and fifth arches, which will be described below. On the dorsal border of the ceratobranchial of the first arch there

are seven toothed gill rakers, with small bony toothplates lying between them; there are one or two gill rakers which articulate in the area where the epibranchial and the ceratobranchial are joined. The second ceratobranchial carries five gill rakers, with a sixth lying in the area of articulation between the epibranchial and the ceratobranchial. Ceratobranchial 3 bears five gill rakers, also with bony tooth plates between them; another gill raker lies in the area of the epibranchial-ceratobranchial articulation. Ceratobranchial 4 bears numerous tooth plates on its anterior border, but no gill rakers. The fifth ceratobranchial bears numerous toothplates on its anterior border and small conical teeth on its dorsoposterior border; these teeth extend more anteriorly on the anterior portion of the bone.

The hypobranchial of the first arch is a relatively large bone that has a medially-directed anterior ramus which diarthrodially articulates in the area of articulation between the first and second basibranchials (Fig. 10). Posteriorly, it articulates diarthrodially with the ceratobranchial. Lateral to the medially-directed ramus of the hypobranchial there is a large articulation surface for a ligament (see below). The bone bears two well-developed toothed gill rakers and two or three tooth patches on its dorsal border. There are also two or three elongate tooth patches on the connective tissue covering the ligament which extends from the anterodorsal border of the hypobranchial to the anteromedial surface of the dorsal hypohyal. There are three or four small tooth plates on the ventromedial surface of the bone.

Hypobranchial 2 is shorter than hypobranchial 1. It also has a medially-directed ramus which has a large concave surface which diarthrodially articulates in the area of articulation between the first and second basibranchials (Fig. 10). Anterolaterally, there is a large articulation surface for a ligament (see below). The dorsal border of the hypobranchial bears two large gill rakers and two toothplates. There is also a series of approximately eight or nine toothplates that are attached to the connective tissue that overlies the ligament which extends between the articular point on the anterolateral surface of the hypobranchial and the posteromedial surface of hypobranchial 1. There are two or three tooth patches on the posteroventral surface of the bone.

Hypobranchial 3 is tightly bound to the third basibranchial (Fig. 10). Anteriorly, the bone extends along the ventrolateral surface of the basibranchial and has a slender ossified ramus which continues as a cartilage body to attach to the posteromedial surface of hypobranchial 2; these bilateral rami nearly meet at the ventral midline and form a broad perichondral ossification laterally over basibranchial 3. More posteriorly hypobranchial 3 is tightly bound diarthrodially to the lateral and dorsal surfaces of basibranchial 3. The posterior border of hypobranchial 3 is deeply concave and articulates diarthrodially with the ceratobranchial of the third gill arch posteriorly and with basibranchial 4 medially.

As mentioned above, ceratobranchials 4 and 5 articulate directly with basibranchial 4.

The basibranchials are median, unpaired bones which are entirely toothless (although toothplates lie in connective tissues adjacent to basibranchials 2 and 3) (Fig. 10). The cartilage cores of basibranchials 1 and 2 apparently are continuous, forming a synchondrosis. The perichondral ossification of basibranchial 1 is more or less oval in cross section. The bone is elongate in an anteroposterior plane, with a broad surface anteriorly where the hypohyal articulates diarthrodially. The ventral borders of the ossifications do not meet, and cartilage is visible along the entire ventral border of the basibranchial. In the area between the ossifications of basibranchials 1 and 2 there are bilateral deep concavities in the

cartilage where the first hypobranchials articulate.

Basibranchial 2 is a perichondral ossification that surrounds the cartilage core (Fig. 10). The ventral bony border is more or less flat in a horizontal plane, with bilateral bony flanges extending from it. Dorsally, the ossification extends anteriorly to overlie the ossification of the posterodorsal surface of basibranchial 1; posteriorly, the bone extends over the ossification of basibranchial 3.

Basibranchial 3 is an elongate cartilage with perichondral ossification (Fig. 10). Ventrally, laterally, and posteriorly there are hypobranchial ossifications articulating with the basibranchial cartilage. Dorsally, there is an elongate perichondral ossification on the surface of the cartilage; anteriorly, this is overlain by bone from basibranchial 2. The cartilage of basibranchial 3 is not continuous with that of basibranchial 1 and 2, but articulates with it diarthrodially. Anterolaterally, basibranchial 3 articulates diarthrodially with the hypobranchials of the second arch.

Basibranchial 4 is a cartilaginous body articulating diarthrodially with basibranchial 3 anteriorly, with the ceratobranchial of the third arch anterolaterally, with the ceratobranchials of the fourth arch laterally, and with the ceratobranchial of the fifth arch posteriorly (Fig. 10).

Retractor Dorsalis Muscle

The retractor dorsalis is a large, bilaterally paired, unsubdivided muscle with its origin on the ventral surfaces of the seventh to ninth vertebrae posterior to the neurocranium and its insertion on the posteromedial surface of the fourth infrapharyngobranchial. See Winterbottom (1974: 256) for a discussion of the nomenclature of this muscle.

Ligaments of the Suspensorium

In *Diplophos* the interpremaxillary ligament is short and very thick, lying far dorsally on the short premaxillary articular process in a pronounced concavity on the medial premaxillary surface (Fig. 12A). The interpremaxillary ligament is unpaired, but all other ligaments described below are bilaterally paired. The premaxillary-rostrodermethmoid ligament is well developed and extends from the anterior border of the rostrodermethmoid, just lateral to the midline, primarily to the ventromedial surface of the contralateral premaxillary bone; some of the fibers extend to the ventromedial surface of the ipsilateral premaxilla (Fig. 12B). The anterior premaxillary-maxillary ligament extends from the ventral border of the maxilla to the posterior surface of the premaxilla on the articular process, lateral to the attachment site of the interpremaxillary ligament (Fig. 13). The posterior premaxillary-maxillary ligament extends from the dorsolateral surface of the maxilla, where that bone extends ventral to the premaxilla, to just ventral to the dorsal border of the premaxilla, at about the level of the second premaxillary fang (Fig. 14).

A premaxillary-rostral cartilage ligament extends from the posteroventral surface of the rostral cartilage to the posterior surface of the premaxillary bone near the attachment site of the anterior premaxillary-maxillary ligament (Fig. 13). The anterior palatomaxillary ligament extends as a short broad sheath from the anterolateral border of the cartilaginous palatine head to the dorsal surface of the maxilla near its anterolateral border, at about the dorsal midline of the bone. The medial palatomaxillary ligament extends from the anterolateral surface of the palatine teeth to the medial surface of the maxillary bone (Figs. 13, 14). The posterior palatomaxillary ligament extends anterolaterally from a point on the palatine bone posterolateral to the attachment site of the anterior palatomaxillary ligament (at about the level of the third to sixth palatine teeth) to the dorsolateral surface of the maxillary bone.

The antorbital-maxillary ligament extends anteroventrally from the postero-

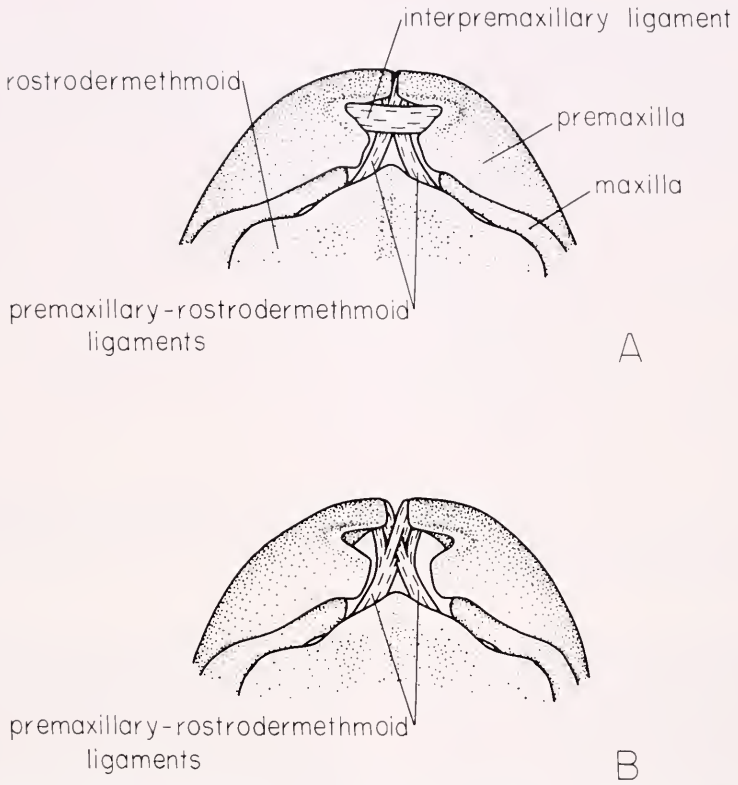

Figure 12. Anterior ligaments of suspensorium of *D. taenia* (USNM 206908; 184.3 mm SL), dorsal view. A. Interpremaxillary ligament in place. B. Interpremaxillary ligament removed.

ventral border of the antorbital to the maxilla, attaching just anterior to the anterior palatomaxillary ligament (Fig. 14).

The palatovomer ligament is broad, consisting of two primary bodies, one of which extends from a ventral prominence at the base of the anterior palatine tooth to the posterolateral border of the vomer; the second body extends between the posterolateral border of the vomer and the ventromedial edge of the palatine bone between the anterior palatine tooth and the anterior bony border of the palatine bone (Fig. 13). Both bodies of the palatovomer ligament are more or less continuous with one another. A well-developed palatine-lateral ethmoid (posterior surface) ligament extends from the dorsal surface of the palatine bone, at about the level of the medial palatomaxillary ligament, to the posterior surface of the ethmoid bone (Fig. 14).

Adductor Mandibulae Muscles

In *Diplophos* the adductor mandibulae muscle is subdivided (Fig. 15A, B). The major, mostly lateral, division (A_2, A_3) is a large, fan-shaped muscle with its origin on the ventrolateral surface of the hyomandibula and the anterolateral face of the preopercle; the muscle inserts, largely via a tendon, on the medial face of the anguloarticular near the posterodorsal border of the coronoid process. A few fibers have their origin medial to the smaller adductor division described immediately below; some anterior fibers insert on the primordial ligament (see below and Fig. 15B). The smaller, medial,

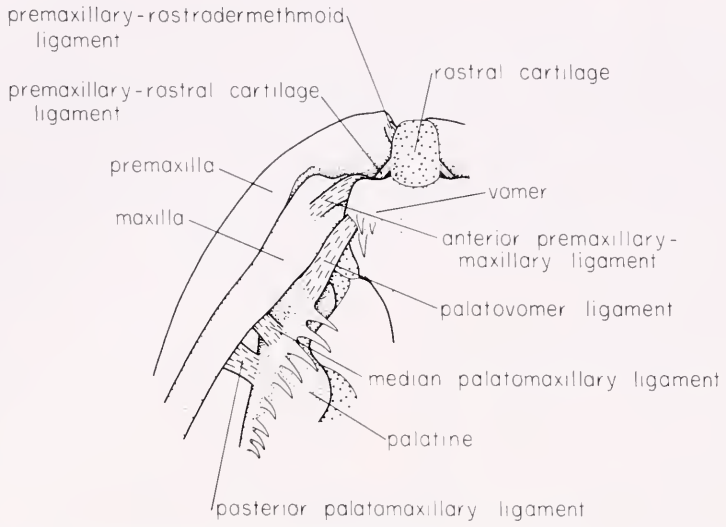

Figure 13. Ligaments of the suspensorium of *D. taenia* (USNM 206908; 184.3 mm SL), ventral view; maxilla and premaxilla spread slightly laterally; teeth of those bones not depicted.

division of the adductor consists of two sections, one dorsal and one ventral, each with origins on the posterolateral surface of the hyomandibula, quadrate, and metapterygoid (Fig. 15B). The dorsal section also has its origin in a raphe with the levator arcus palatini; it inserts on the dorsal border of the maxilla, just anterior to the mid-length of that bone; in small specimens there may be a fascia from the main muscle body to the insertion on the anterior supramaxilla and maxilla. The ventral section inserts on the primordial ligament. The dorsal attachment of the primordial ligament is on the lateral surface of the maxilla, anterior to the insertion of the dorsal section. The ventral insertion is on the lateral surface of the anguloarticular near its articulation with the quadrate. There is a tendon closely uniting the posterior supramaxilla to the primordial ligament. The fibers of the ventral section ventrally merge with those of the lateral division.

The fibers of the medial adductor muscles are virtually indistinguishable proximally, forming a continuous fan of muscle, and in our specimens they can be identified only by their insertions.

The intramandibular division (Aω) (not illustrated) of the adductor mandibulae has its origin on the anterior border of the tendon of the lateral division of the adductor and its insertion along the medial surface of the anguloarticular and dentary bones.

Postcranial Axial Skeleton

All counts except when otherwise designated are from *D. taenia*, USNM 206614. Counts for *D. maderensis*, USNM 186364, are given in parentheses.

The anterior element of the postcranial axial skeleton is the accessory neural arch (Fig. 5). Dorsally each arch element is unfused to its counterpart of the contralateral side. The joint between the arches is strongly bound by fibrous connective tissue and the dorsomedial apposing surface of each arch faced by cartilage. The entire arch encloses the dorsolateral surface of the spinal cord as it exits the cranium. The anterior and anteroventral

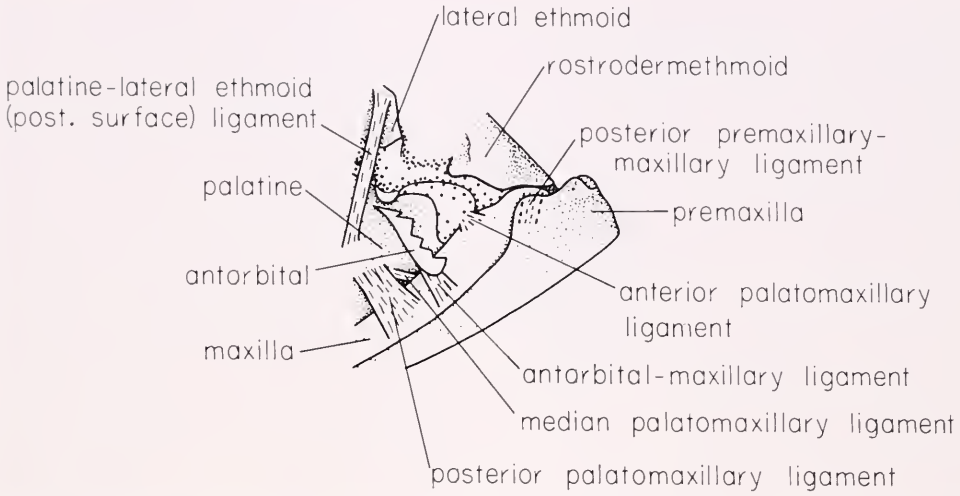

Figure 14. Ligaments of the suspensorium of *D. taenia* (USNM 206908; 184.3 mm SL), lateral view; antorbital bone partially removed; teeth not depicted.

borders of each arch element are bound by a sheet of strong fibrous connective tissue to the posterior arch-like face of the exoccipitals. This connective tissue sheet encloses the dorsal and lateral portions of the spinal canal and its contents. Ventrally, strong fibers of connective tissue bind each arch to the thick fibrous connective tissue between the anterior (first) vertebra and the exoccipital. Posteriorly, the border of the entire arch is joined by a sheet of connective tissue to the neural arch of the first vertebra. Successive neural arches are connected to each other in a similar manner.

There are 87 (63) vertebrae. Mukhacheva (1978) summarizes vertebral counts for *Diplophos* species. The first vertebra consists of an amphicoelous disc-shaped centrum associated with autogenous dorsolaterally-articulated neural arches and ventrally-articulated parapophyses. These structures are firmly bound by fibrous connective tissue to the relatively deep fossae which they fill. The neural arch of each side dorsally meets its counterpart in the same manner as the accessory neural arch. The neural arches are anteroposteriorly broad along their dorsal border. The posterior border of the neural arch is fused with a short neural spine which is unfused to the spine of the contralateral side. Well ventrally on the posterior area of the neural arch at the anterior base of the neural spine is a slender epineural, which extends laterally and posterodorsally into the myocommata for the length of three to three and a half centra.

The parapophysis of the first vertebra bears a spinous process extending somewhat ventrally and posterolaterally. This process is continuous with Baudelot's ligament described below with the pectoral girdle. The postzygapophysis is located on the body of the centrum just posterior to the base of the neural arch. The first vertebra is separated from the exoccipitals and the centrum-like posterior facet of the basioccipital by a narrow space. The anterior border of the centrum is attached to the posterior exoccipital and basioccipital facets by thick fibrous connective tissue. The bodies of the first and second centra are closely approximated and their borders are bound together by

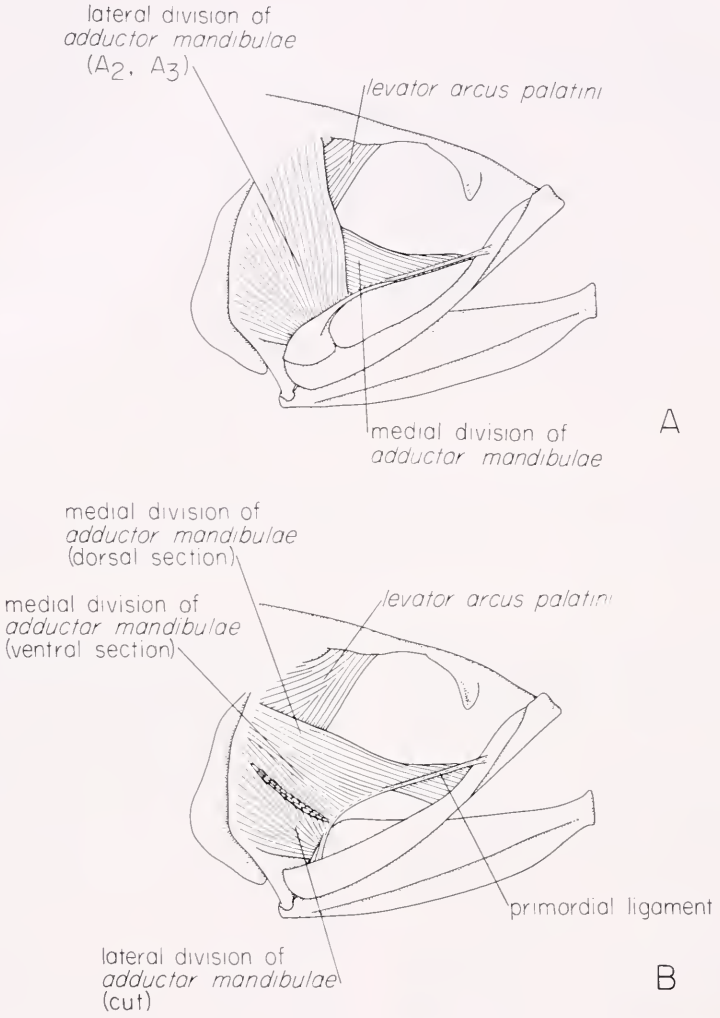

Figure 15. Adductor mandibulae muscles of *D. taenia* (MCZ 55469; 117.0 mm SL). A. Lateral division present. B. Lateral division removed to show underlying muscle.

strong fibrous connective tissues, as are those of all the successive centra.

The second vertebra is much the same as the first, but anteriorly the basal portion of its neural arch bears a prezygapophysis which has a medial face articulating with a posterolateral face of the postzygapophysis of the first vertebra.

The neural arches and spines of the second through the fourth vertebrae are similar in shape and articular relationships to those of the first vertebra. The fifth (third) and successive vertebrae gradually diminish the broad dorsal border of the arches until by the eighth (sixth) vertebra these arches taper to their respective spines. The spines remain unfused until the 39th (30th) vertebra is reached. The spine of this vertebra inserts between the last two pterygiophores of the dorsal fin of *D. taenia*, but in *D. maderensis* it inserts between the

eighth and ninth pterygiophores. The second radial rod of the anterior dorsal fin pterygiophore passes between the 32nd (23rd) and 33rd (24th) vertebral spines. The last neural arch to directly bear an epineural is number 36 (29). Two (six) neural arches posterior to this bear short epineurals attached by moderately long ligaments. The last vertebra with a neural arch not fused to the centrum body is number 35 (29). The 36th (30th) vertebra has the neural arch entirely fused to the body of the centrum, as do the remaining centra, except the arches of the ural centra (see description of the caudal complex below).

The pattern of articulation between the dorsal post- and prezygapophyses described above for the first and second vertebrae is continued posteriorly through the entire vertebral column. However, only the first four or five (six or seven) vertebrae have the zygapophyses overlapping. In the more posterior vertebrae these processes approach each other with their respective anterior and posterior ends nearly abutting and bound to each other by fibrous connective tissue.

Parapophyses of the first through the 34th (27th) vertebrae are not fused to the centra. The 35th vertebra is the only vertebra to bear a fused parapophysis. There is no fused parapophysis in the *D. maderensis* examined.

The parapophysis of the second vertebra bears a short ventrolateral process which has fibrous ligaments extending into the associated ventral myocommata. The parapophysis of the fourth vertebra is the first to bear a pleural rib. This is attached to a short process of the parapophysis by fibrous connective tissue. The last parapophysis to bear a pleural rib is that of vertebra 35 (28). This vertebra marks the termination of the abdominal vertebrae.

The 36th (29th) vertebra bears a hemal arch and spine with the spines of each side ventrally fused, marking the beginning of the caudal vertebrae. The rib of the 22nd (15th) vertebra is the first to bear an ossified epipleural and the rib of the 42nd (35th) vertebra is the last to bear such a structure. The tip of the hemal spine of the 38th (30th) vertebra lies just dorsal to the first anal-fin pterygiophore. Ventral zygapophyses are absent or nearly absent on vertebrae dorsal to the abdominal cavity. Abruptly posterior to or just dorsal to the posterior area of this cavity, narrow, small ridges of bone are located ventrolaterally on the anterior and posterior parts of the body of the centra. These ridges progressively enlarge posteriorly until near the mid-region of the caudal vertebrae they form small pre- and postzygopophyses that nearly abut each other. These processes are joined by rather weak fibrous connective tissue.

There are 16 (USNM 206614) or 17 (USNM 206908) supraneurals in *D. taenia* and 13 (USNM 180364) supraneurals in *D. maderensis*. The anterior supraneural in both species is an elongate, somewhat compressed rod of cartilage surrounded by a thin tube of bone except for its proximal and distal ends. This supraneural narrows near its mid-length, but anteriorly in this area has a thin blade-like ridge of bone. The proximal end of the anterior supraneural articulates with the anterior dorsal portion of the neural arch of the first vertebra. The distal end of the supraneural lies just beneath the skin at the midline of the back.

The remaining supraneurals in both species are small, slender cartilaginous rods surrounded by thin bone and lie between the neural spines of vertebrae 2 through 17 in *D. taenia*, USNM 206614.

Caudal Skeleton

The caudal skeletons of *Diplophos maderensis* (Fig. 16) and *D. taenia* are essentially the same except that *D. maderensis* has about 10–13 procurrent dorsal-fin rays, *D. taenia* about 5–6. Only the caudal skeleton of *D. maderensis* is described below.

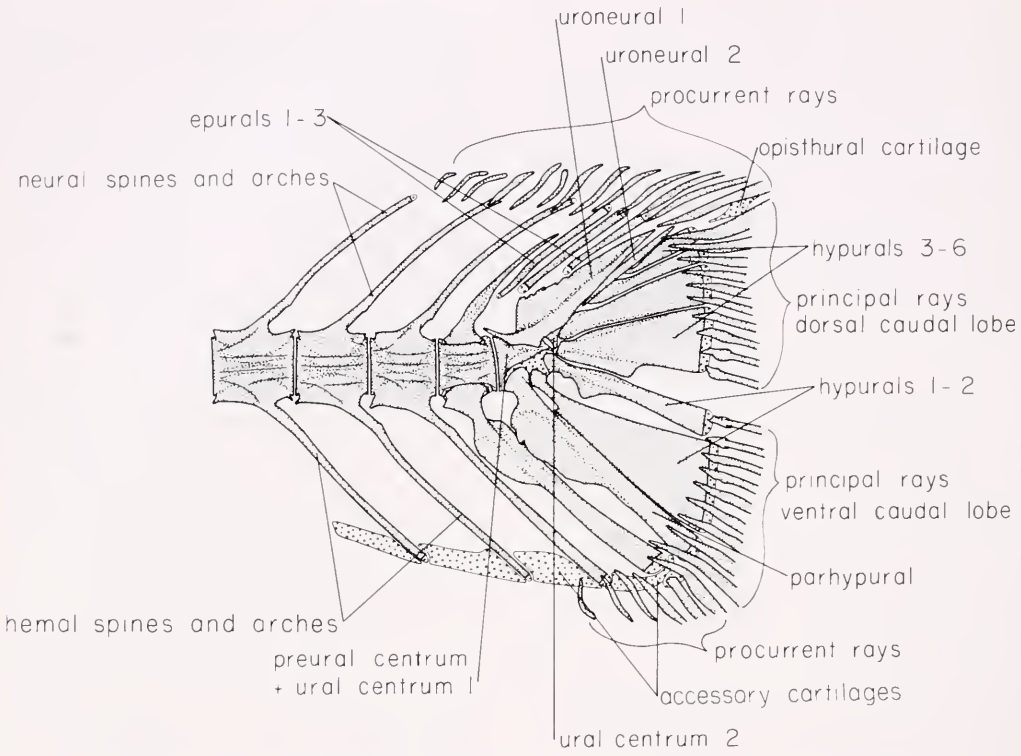

Figure 16. Caudal skeleton of *D. maderensis* (USNM 186282; 111.5 mm SL), lateral view.

A compound centrum consisting of the first preural and first ural centra posteroventrally supports the autogenous parhypural and first and second hypurals. Hypurals three through six are autogenous and separate from each other and lie posterior to the second ural centrum. There is an opisthural cartilage posterior to the sixth hypural, between the posterior dorsal procurrent fin ray and the dorsal principal caudal-fin ray. The neural spine of the first preural vertebra and the first uroneural are autogenous, separate from the fused preural and ural centra below and the second ural centrum posteriorly. A splint-like second uroneural lies posterior to the first uroneural. There are three epurals dorsal to the first uroneural. The bases of the neural and hemal arches of the second preural centrum are autogenous, not fused to the centra as they are in the more anterior caudal vertebrae. A urodermal and third uroneural are absent.

The five terminal caudal vertebrae support the caudal-fin rays but only the neural spines of the third through the fifth preural centra directly support dorsal procurrent rays. The ventral procurrent rays are primarily supported by cartilaginous radials associated with hemal spines borne by the second through the fourth preural centra. Large cartilaginous radials are found between the distal tips of the hemal spines that occur posterior to the termination of the base of the anal fin. There are 10 plus 9 principal caudal-fin rays.

Vertical Fins

In *Diplophos taenia* and *D. maderensis*, the basic osteological unit of the ver-

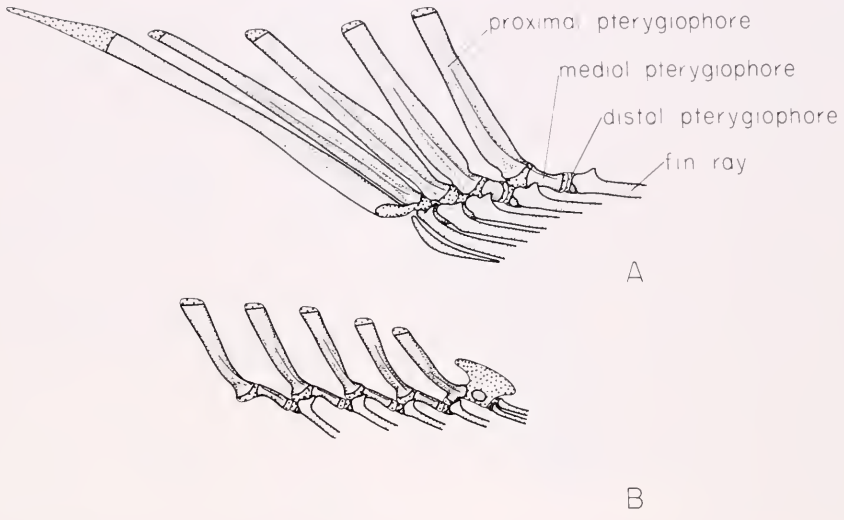

Figure 17. Anal fin skeleton of *D. maderensis* (USNM 186282; 111.5 mm SL). A. Anterior fin base. B. Posterior fin base.

tical fins is the pterygiophore series (Fig. 17A, B). Most of the fin base consists of pterygiophores with three sections: a proximal pterygiophore ossification, a medial pterygiophore ossification (both these ossifications over a single cartilage core), and a cartilaginous distal pterygiophore with bilateral perichondral ossification centers lying between the fin ray halves. The proximal pterygiophore is perichondrally ossified proximally and endochondrally ossified near its distal termination. The anterior and posterior portions of the fins have some modifications, as follows.

In the anal fin, the anterior two proximal pterygiophores are elongate rods which are fused together distally at their cartilaginous tips. The distal portion of the anterior rod of this pterygiophore is expanded bilaterally. The first and second fin rays articulate ventral to the distal cartilage; the second fin ray articulates with the anterior of the first (anterior) distal pterygiophore. Fin ray three lies ventral to the third pterygiophore series and also articulates with the anterior cartilaginous distal pterygiophore. The fourth pterygiophore series consists of a proximal pterygiophore and a block-like medial pterygiophore; the fifth pterygiophore series has a more elongate medial pterygiophore, as do posteriorly successive pterygiophore series. The distal cartilage of the posterior pterygiophore is expanded posterodorsally and has small bilateral ossification centers; the posterior two fin rays share a single distal pterygiophore which articulates with the expanded medial cartilaginous pterygiophore.

In the dorsal fin of *D. taenia*, the anterior pterygiophore series is a tripartite structure that appears to be the fusion of two or three proximal pterygiophore elements. This compound structure is composed of an anterodorsally extended bony flange that in some specimens is rod-like dorsally, and two anteroventrally projecting rods, interconnected by a thin bony flange. Distally the anterior pterygiophore series is capped by a block of car-

tilage. A cartilaginous distal pterygiophore lies posterodorsal to the anterior proximal pterygiophore complex; the distal pterygiophore has bilateral ossification centers along its posterolateral surfaces. The first (anterior) and second fin rays articulate with the anterior distal pterygiophore. The distal cartilaginous cap of proximal pterygiophores two and three are more elongate than that of the first proximal pterygiophore; the posterior cartilaginous extension of proximal pterygiophore four has a medial pterygiophore ossification, as do posteriorly successive pterygiophore series, except for the posterior three to five.

Data on numbers of rays composing the vertical fins of *Diplophos* species are available in Johnson (1970) and Mukhacheva (1978).

Pectoral Girdle

There are two extrascapulars, both consisting of tube bones and very little surface plate (Figs. 3, 4, 7, 8). The medial extrascapular is a short to moderately long open-tubed bone with its long axis nearly parallel with the posterior border of the parietal. A larger L-shaped lateral extrascapular has a long horizontal ramus and a short dorsomedial ramus which connects with the medial extrascapular. The lateral extrascapular is mostly an open tube, but in large adults it is closed superficially at the anteroventral junction of its two rami (Fig. 8). The sensory tube within the extrascapulars connects anteriorly with that of the pterotic and posteriorly with that of the posttemporal. Dorsally it exits from the medial extrascapular and extends a short distance in a groove on the external surface of the parietal. The extrascapulars of *D. maderensis* are almost exactly the same as those of *D. taenia*.

The posttemporal is well ossified and has blade-like anterodorsal and anteroventral principal rami (Fig. 4). The large dorsal ramus is articulated by a short strong ligament to the posterodorsal process of the epioccipital. The narrower and shorter anteroventral ramus is attached by a strong ligament to the central knob-like process of the intercalar. A third, short posteroventral ramus is broadly attached to the dorsolateral surface of the supracleithrum by a short ligament. The posttemporal contains a laterosensory canal extending posteroventrally from the posterior, long ramus of the lateral extrascapular through the posteroventral ramus of the posttemporal. This canal is ventrally continuous with the laterosensory canal of the supracleithrum.

The supracleithrum is an elongate, fairly slender blade-like bone with the lateral face dorsally attached by a short strong ligament to the ventromedial articular surface of the posttemporal. The dorsal ramus of the cleithrum articulates with the medial surface of the supracleithrum. This articulation is extensive, including approximately the ventral half of the supracleithrum. The dorsal apex of the cleithrum lies immediately internal to the central portion of the posterior border of the supracleithrum. The supracleithrum bears a laterosensory canal along its posterior border for about one-third of its total length. Ventral to this canal, the entire posterior border of the supracleithrum continues as a groove, part of which bears a laterosensory canal. The laterosensory canal of the supracleithrum of *D. maderensis* is very similar to that of *D. taenia*.

The cleithrum is a large, complex bone which may be considered in three parts: a dorsal ramus, a body or central portion, and a ventral ramus. The dorsal ramus ends in a conical slender process attached as described above to the medial face of the supracleithrum. Ventrally the cleithrum widens anteroposteriorly to become a broad blade with a rugose or pitted lateral surface, especially anteriorly. The ventral portion of this blade abruptly turns anteriorly to become part

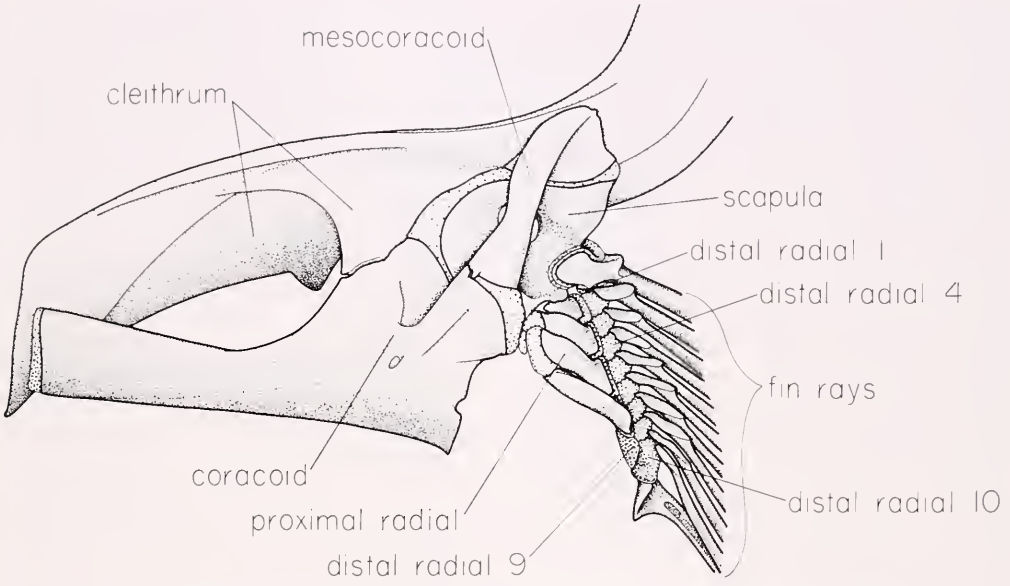

Figure 18. Pectoral girdle of *D. taenia* (USNM 206614; 171.0 mm SL), dorsomedial view.

of the body of the cleithrum which articulates with the pectoral girdle bones bearing the radials and fin rays (Fig. 18). A cross section near the mid-length of the blade-like portion of the dorsal ramus of the cleithrum is rounded anteriorly and abruptly narrower posteriorly. The posterior blade-like portion tapers to a thin edge posteriorly. The lateral wing of the cleithrum extends from the blade-like dorsal ramus of the cleithrum, continues as the lateral blade-like portion of the body of the cleithrum and extends forward as the main part of the anterior blade-like part of the cleithrum (Fig. 18). The body of the cleithrum bears a moderate sized medial wing which extends to contact the coracoid and scapula (Fig. 18). The anterior ramus of the cleithrum is a broad dorsoventrally placed sheet of bone which is anteriorly attached by ligaments to the cleithrum of the contralateral side and to the anterior coracoid ramus.

In some stomiiforms the major ligaments of the pectoral girdle become much modified, and for that reason particular attention is paid to them here. The ligaments of the posttemporal-cranial and the posttemporal-supracleithrum articulations were described above. The ligaments described below are numbered for ease of future reference. The supracleithrum and cleithrum are bound by a broad, very short ligament (1) which extends from the ventromedial surface of the supracleithrum to the dorsolateral surface of the cleithrum. This joint lies somewhat ventral to the region of the cleithrum where it narrows into a conical process.

Baudelot's ligament, ligament 2, extends posteriorly from the anterior vertebral centrum, passes medial to and wraps around the dorsal process of the cleithrum without attaching to it, and connects to the medial surface of the supracleithrum. This ligament is anteriorly attached to a ventrolateral extension of the parapophysis of the anterior vertebral centrum. This bony process extends nearly one-third to one-half of the distance from the centrum to the distal termination of the ligament.

The cartilaginous coracoscapular plate

and its ossifications in *Diplophos* are typical of many teleosts (see Starks, 1930) (Fig. 18). The cartilage body of the plate projects from the medial surface of the body of the cleithrum at its curvature. The coracoid bone, the anterior portion of the cleithrum, and the medial wing of the cleithrum surround a large coracoid aperture. The term coracoid aperture is used for this space because previous names for it, such as coracoid-cleithral foramen (Rendahl, 1933) and interosseus space (Starks, 1930) are inadequate to describe the various coracoid morphologies found in the stomiiforms. The coracoid cartilage is covered by well-ossified bony lamellae forming the coracoid bone. The coracoid is an L-shaped bone with a long anterior ramus meeting the cleithrum near its anteroventral termination. It has a broad lateral ramus contacting the medial cleithral wing. The anterior ramus terminates in cartilage. The coracoid articulates posterolaterally in a synchondral joint with the scapula. A short dorsolateral ramus is continuous with the cartilaginous base of the mesocoracoid. Anteriorly the coracoid and mesocoracoid contact each other in this area. The posteromedial ventral spinous process of the coracoid is short and blunt, not elongate as described for *Astronesthes niger* by Weitzman (1967b: 29). Both the anterior ramus and the short spinous process are flattened lateromedially.

The scapular ossification of *Diplophos* is composed of thin layers of bone, one dorsal and one ventral, which sandwich the posterolateral area of the coracoscapular plate (Fig. 18). The two bony layers meet and form a continuous bony surface along the posterior scapular border. There is an articular surface along the posterior scapular border for the proximal articular surface of the first pectoral-fin ray and proximal radial I (the lateral proximal radial, described below). The lateral portion of the scapula lateral to the scapular foramen extends vertically, and it articulates with the coracoid. Medially the scapula extends in a plane that dips ventrally in a posteromedial direction. The scapula medially connects to the coracoid through a synchondral joint. The scapular foramen is entirely enclosed by bone.

The fully developed mesocoracoid of *Diplophos* is much like that of other teleosts as described by Starks (1930) (Fig. 18). The mesocoracoid is a tube of thin bone surrounding a rod of cartilage that extends from the coracoscapular plate at the posterior border of the coracoid and the scapula and laterally articulates with the medial surface of the cleithrum near the midpoint of the central curvature. A ventrolateral ramus of the lateral end of the mesocoracoid extends from its junction with the cleithrum as a sheet of bone over the medial surface of the cleithrum at its central curvature.

Herein, proximal radials are designated by Roman numerals (I–IV) and distal radials by Arabic numerals (1–10).

Proximal radial I is the most lateral of the proximal radials. It is proximally associated with the scapula and coracoscapular plate. Radials II, III, and IV are medially placed in succession. Radials II and III are in association proximally with the cartilaginous coracoscapular plate while radial IV is free of the plate.

Diplophos taenia has radial I short and with well-ossified bone around a central cartilaginous core (Fig. 18). There is exposed cartilage anterolaterally on radial I where it articulates with the medial border of the scapula and to a lesser extent with the cartilaginous border of the coracoscapular plate. There is also exposed cartilage distally on radial I where it articulates with distal radials 2 and 3. Medially, radial I articulates with radial II. Distally, radial I articulates with distal radial 2 and partially with 3. Radials II and III are much longer than radial I, with III being the longest. Both radials II and III have their proximal and distal ends of cartilage; they articulate proximally with the cartilage of the coracoscapular plate and distally with distal ra-

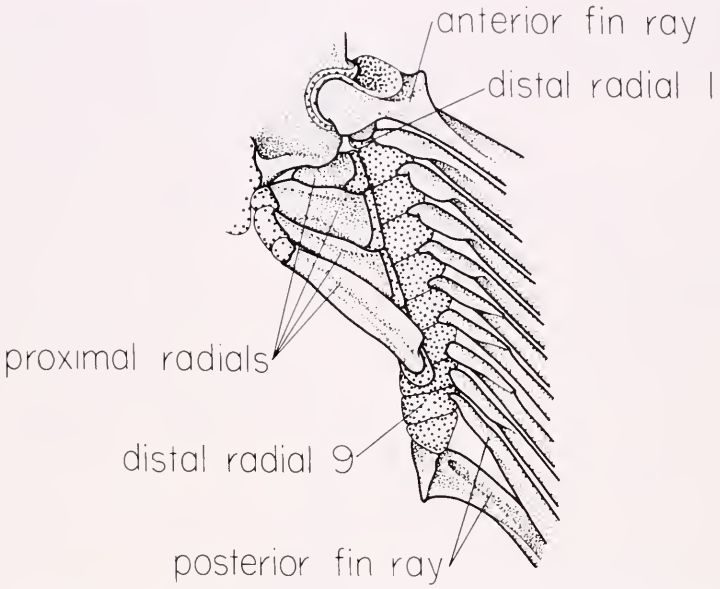

Figure 19. Pectoral radials and fin rays of *D. maderensis* (USNM 186282; 111.5 mm SL), dorsomedial view.

dials 3–4 and 5–6, respectively. Distally, radial IV articulates with distal radials 7–9; proximally, it articulates in an apparently immobile joint with radial III as part of a proximal radial plate between the coracoscapular plate and the distal radials (this morphology is also present in *D. rebainsi*). Radial IV has a flange of thin, plate-like bone arching dorsomedially.

There are ten distal radials and ten fin rays in *D. taenia* (Fig. 18). The anterior distal radial (1) lies between the base of the ray halves of the large first pectoral-fin ray. The cartilage of this radial is firmly set on a short pedicel of bone of the dorsal ray half and articulates medially with distal radial 2 as well as with proximal radial I. The remaining nine distal radials are free of their respective fin rays and are articulated with them in a movable joint. There is one distal radial for each fin ray, and, except for radial 9, each ray has its dorsal half articulating with the dorsal anterolateral area of the distal radial and its ventral ray half articulating with the ventral posteromedial area of the distal radial. Radial 9 lies dorsomedial to radials 8 and 10, which articulate directly with each other. (In *D. rebainsi* distal radial 8, also the second from last, is likewise dorsomedial to its adjacent radials.)

The proximal and distal radials of *D. maderensis* (Fig. 19) differ from those of *D. taenia*. Proximal radials III and IV have separate cartilage cores, as in those of most teleosts. Proximal radial IV has a small ventral longitudinal flange, missing in *D. taenia*, and a somewhat smaller dorsal longitudinal flange than *D. taenia*. The relative plesiomorphic versus apomorphic nature of these flanges has not been determined. The ten distal radials of *D. maderensis* and their respective fin rays are arranged as in *D. taenia* except that distal radial 9 is in series with the other radials and bears the same relation to its fin ray as do radials 2 through 8. The articulation of proximal radial IV is directly with distal radials 6 through 8. Outgroup comparison indicates that the

condition of the distal radials in *D. maderensis* is plesiomorphic relative to that of *D. taenia*.

Pelvic Girdle

The pelvic girdle of *Diplophos* (Fig. 20) consists of two pelvic plates which are small relative to body size and are well ossified. Medially, the pelvic plates are bound closely together by connective tissue for most of their length, but they touch only at the anterior cartilaginous processes. They lie at an angle of about 45° to each other, with the apex dorsal. The anterior cartilaginous process is a short rounded extension of cartilage from the core of the anterior process just posterior. The anterior process is a long, narrow bony rod, cartilage-filled, which is slightly larger distally than proximally. The medial pelvic plate, a thin lamella of bone, extends along almost the entire medial border of the anterior process, and posteriorly joins the anterior border of the posterior plate; its medial border is slightly concave. A small lateral anterior plate extends between the proximal one-third of the anterior process and the lateral process. The anterior portion of the posterior plate consists of a short, medially directed bony rod, cartilage-filled; the medial surface of this rod is unossified. The anterior border of the rod lies at an angle of about 100–110° to the longitudinal axis of the pelvic plate. Posterior to this cartilage-filled rod, the posterior plate consists of a thin rugose lamella. In *D. taenia*, this lamella is endochondrally ossified to the posterior border of the basipterygium; in *D. maderensis*, a narrow cartilage border is present distally on this lamella. The posteromedial border of the posterior plate is deeply convex. The posterior border of the posterior plate joins the lateral process anterolaterally. The endochondrally ossified lateral process is short and broad and forms the lateral bony border of the basipterygium; lateral to it is the lateral cartilaginous process, against which articulate the radials. There are three radials. The anterior two lie lateral to the lateral cartilaginous process, and the third, posterior, radial lies posterior to the cartilaginous process and lateral to the posterior plate. Radial 1, the anterior of the three, slightly smaller than the others, is an oval cartilage with dorsal and ventral ossification centers. Radial 1 lies between the ray halves of the first and second rays. Radial 2 is similar in structure to radial 1 and is associated with rays three through six. Radial 3 is a hemispherical cartilage anteriorly and is ossified posteriorly, tapering to a blunt, short process. This radial is associated with rays seven and eight. There are eight fin rays, all segmented with relatively short segments. Ray one is shortest and unbranched. The remaining rays are branched. Rays two and three are progessively longer, and rays four through eight progressively shorter, with ray eight about 75% of the longest ray (*D. taenia*).

The identity of actinopterygian pelvic girdle elements has been discussed by Stensio (1921, 1925) and Rosen *et al.* (1981), among others. Further investigations are needed to establish the homologies of actinopterygian and non-actinopterygian girdle elements, especially those of the pelvic plate proper and radial 3, which may be a metapterygial element.

RELATIONSHIPS OF THE STOMIIFORMES

At various times in the past, stomiiforms have been considered non-monophyletic, or monophyletic and related either to various primitive teleostean groups (protacanthopterygians, isospondyls, etc.) or to more derived teleosts (Eurypterygii of Rosen, 1973) (Fig. 21). Present evidence indicates that the group is monophyletic and corroborates a sister group relationship with the Eurypterygii.

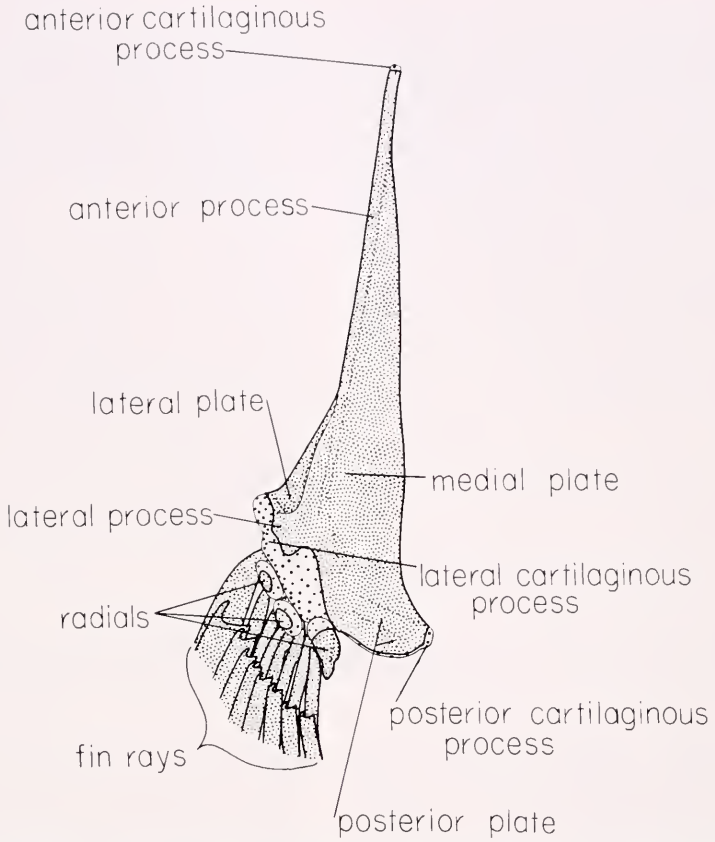

Figure 20. Pelvic fin girdle of *D. maderensis* (USNM 186282; 111.5 mm SL), ventral view; ventral fin ray halves removed proximally to show radials.

Monophyly of the Stomiiformes

The morphological diversity of species now placed in the Stomiiformes has historically presented problems to systematic ichthyologists. The morphological differences between, say, *Argyropelecus* (see Weitzman, 1974, Figs. 11 and 12; Schultz, 1964, Fig. 64) and *Malacosteus* (see Morrow, 1964b, Fig. 144) confounded many early workers and led them to place various genera with groups now removed to other positions in our hypotheses of teleostean phylogeny. Most diagnoses of the group have included the presence of photophores and a combination of other features which are distributed widely among primitive teleosts (see Regan, 1923; Morrow, 1964a; Weitzman, 1967a; and our discussion concerning Greenwood *et al.*, 1966, below). So far as we are aware, the monophyly of the Stomiiformes has never been explicitly documented by characters unique to the group. The Stomiiformes can be diagnosed by the presence of the following characters:

1) Photophores with a structure unlike that of other teleosts. Bassot (1966, 1970) has described stomiiform photophores histologically and found that they are composed primarily of two cell types, designated by him as A and B. Type A cells, typified in part by the well-developed endoplasmic reticulum, apparently produce the luminescent product (see Herring and Morin, 1978). More recent works on the histology of stomiiform light

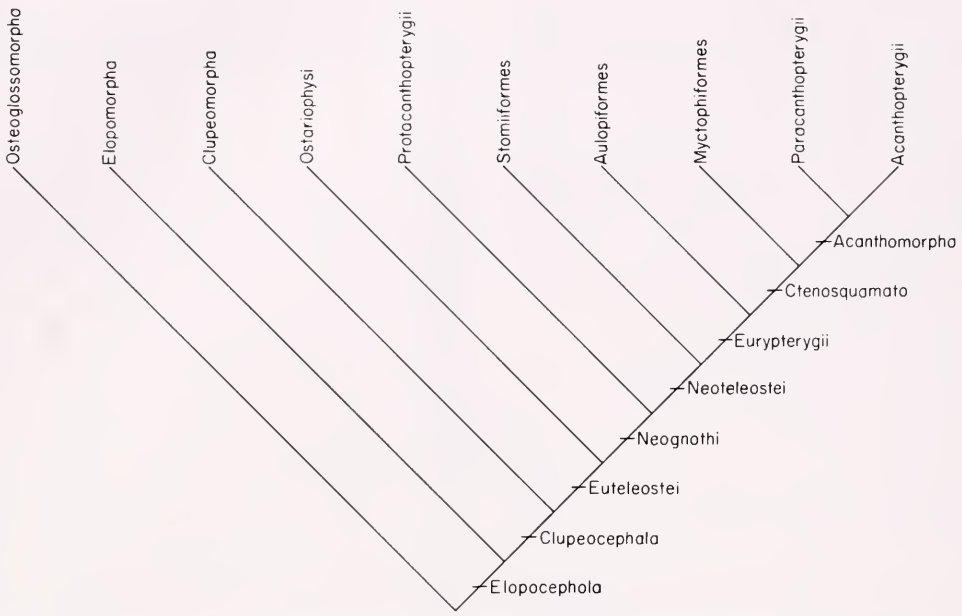

Figure 21. Recent concepts of phylogenetic relationships among the major teleostean lineages. Hypothesis of euteleostean relationships of Rosen (1973); non-euteleostean relationships hypothesized by Patterson and Rosen (1977).

organs include Jørgensen and Munk (1979), Hansen (1970), and O'Day (1973). Stomiiform photophores are non-bacterial (Herring and Morin, 1978; see also Baguet and Marechal, 1976).

According to Bassot (1970), stomiiform photophores can be described as follows: The walls of the photophores are formed of flat conjunctive cells filled with guanine platelets and covered laterally by a pigmented layer. This wall thus serves as a reflector. A gelatinous body appears to serve as a lens. The interior of the photophore consists of two cell types, A cells, the photocytes, which are densely packed and fill most of the photophore, and B cells, which Bassot describes as "glandular." Bassot notes that the properties of the photocytes are the same in all stomiiforms he examined. In primitive stomiiforms the photocytes are arranged roughly perpendicular to the center of the photophore, where there is a lumen (opening to the outside in the most primitive species); this is Bassot's Type Beta photophore. In more specialized species, the lumen is not present and the photocytes are arranged either perpendicular to the center of the photocyte region (Type Gamma photophore) or are arranged in successive rows perpendicular to the main axis of the photophore (Type Alpha photophore). Weitzman (1974) noted that the distribution of the three photophore types corresponds well to his alignment of the sternoptychids, gonostomatids, and photichthyids and noted that, within the context of his proposed phylogeny, Bassot's Type Beta photophore is probably primitive for stomiiforms, while Types Alpha and Gamma are derived.

Some other teleosts have photophores, but none have photophores with morphology like those of stomiiforms. In the context of current hypotheses of teleostean phylogeny, photophores have evolved independently in numerous lineages. The following brief survey of non-bacterial photophores is based on the re-

view by Herring and Morin (1978) and is intended only to establish that, according to our knowledge of photophore morphology, the photophore structure of stomiiforms is unique. Much work remains to be done on photophore morphology in teleosts.

Among primitive teleosts, organized photophores are present in a single engraulid (*Coilia dussumieri*; Haneda, 1961) and in four alepocephalid genera, *Xenodermichthys*, *Photostylus*, *Rouleina*, and *Microphotolepis* (Herring and Morin, 1978). Best and Bone (1976) have described photophores of *Xenodermichthys* and *Photostylus* and found them to be unlike those of other teleosts (see their Fig. 2). A single species of *Rouleina* has small flat photophores in juvenile stages (Markle, 1978); these are apparently unlike those of stomiiforms.

Phylogenetically more advanced teleosts with photophores include the aulopiform scopelarchids *Benthalbalba infans* and *Scoperlarchoides kreffti*. Herring and Morin (1978) report that the photogenic tissue in these species is developed from ventral muscle tissues and that light is emitted through the ventral musculature. The evidence that photophores in these species are very different morphologically from those of stomiiforms, combined with lack of evidence that the two genera are more closely related to stomiiforms than to other scopelarchids, indicates that the photophores are independently derived.

Within the Myctophiformes, photophores are known in *Neoscopelus* species and in all myctophid genera and species; species in the two other neoscopelid genera, *Solivomer* and *Scopelengys*, lack photophores. According to Herring and Morin (1978), citing Brauer (1908) and Kuwabara (1954), photophores of *Neoscopelus* are different from those of myctophids. Examination of Brauer's Plate 31 shows that the photophores of *Neoscopelus* are different from those of stomiiform photophores. Myctophid photophores are likewise distinct (see Fig. 9.11 of Herring and Morin, 1978) and different from those of stomiiforms, being relatively flattened and with less glandular tissue. Edwards and Herring (1977) have described photogenic tissues of myctophids as being composed of a number of flattened lamellae (see their Fig. 2).

Non-bacterial photophores are also reported to occur in the paracanthopterygian *Porichthys* and the perciform scaenid *Collichthys* (Herring and Morin, 1978); the phylogenetic remoteness of these genera from stomiiforms precludes further discussion.

Luminous tissues which are not organized into photophores have been reported in many teleostean groups, including stomiiforms. Structure of these tissues at the cellular level is unknown for the most part, and the systematic significance of their structure cannot be evaluated as yet.

2) Type 3 mode of tooth attachment. As defined by Fink (1981), Type 3 mode of tooth attachment has the following characteristics: The anterior mineralized border of the tooth is either close to the attachment bone at the tooth base and bound to it by collagen or ankylosed to the attachment bone. The posterior mineralized border is further from the attachment bone than the anterior border, leaving a larger portion of the posterior surface of the tooth collagenous; this flexible collagenous area is bound to the attachment bone. The tooth is hinged, or depressible, with its axis of rotation being the anterior tooth border.

Adult stomiiforms may have one or two of three modes of tooth attachment: Type 1 (fully ankylosed to the attachment bone), Type 3 (described above), or Type 4 (like Type 3 except the anterior mineralized border is free from the attachment bone and the axis of rotation is the collagenous tissue connecting the posterior tooth border with the attachment bone). Type 1 attachment mode is a primitive feature for teleosts (Fink, 1981).

Type 4 mode is found in juvenile stages of primitive stomiiforms, in the adults of some (perhaps paedomorphic) derived species (e.g., *Pollichthys*, *Vinciguerria*, *Valenciennellus*), and in many neoteleosts. Both Types 3 and 4 attachment modes are apparently the result of changes in the primitive teleostean pattern of tooth ontogeny.

Type 3 attachment mode occurs in adults of most stomiiforms, on either the jaws, the branchial apparatus, or both. On those bones where Type 3 is not found, either Types 1 or 4 are present; both of those modes are primitive for stomiiforms. Type 3 mode has not been found in any other group of teleosts.

3) Presence of a medial division of the adductor mandibulae muscle which is subdivided into two sections, a dorsal one inserting directly onto the maxilla, and a ventral one inserting onto the primordial ligament (Fig. 15A, B). Both the dorsal and ventral medial adductor sections were labelled $A_1\beta$ by Rosen (1973; Figs. 26 of *Astronesthes* and 23 of *Maurolicus*, respectively). Both these sections are present in *Diplophos*. Among many more specialized stomiiforms, one or the other of these is emphasized, and the other is reduced or lost. In a few members of the group, such as *Gonostoma* and *Margrethia*, additional sections are present. From our survey of adductor muscles within the stomiiforms, it appears that these muscles will be useful in analysis of phylogenetic relationships within the group.

Presence of a muscle inserting on the maxillary, either in the form of an A_1 (a dorsolateral division of the adductor mandibulae) or an $A_1\beta$ (a medial division of the adductor mandibulae) was deemed a neoteleostean character by Rosen (1973). We suggest, however, that these muscles are not homologous (at least in non-acanthoptergyian teleosts) and that the mechanism of maxillary control cannot be synapomorphic for neoteleosts. The bases for our hypothesis are morphology and the distribution of other characters (a parsimony consideration). The morphological evidence is that A_1 lies lateral to A_2 while $A_1\beta$ lies medial to A_2. Thus, each muscle probably arises from different parts of the undifferentiated adductor during ontogeny. The distribution of other characters also supports our hypothesis. An A_1 is present in members of all the major eurypterygian lineages (aulopiforms, myctophiforms, paracanthopterygians, and acanthopterygians), indicating that it is a eurypterygian character. The distribution of $A_1\beta$, however, suggests that it has arisen as a neomorphic character several times: in stomiiforms, in myctophids, and at least once in acanthomorphs. In myctophids, for example, an $A_1\beta$ is present (Winterbottom, 1974, Fig. 4), while in the sister group of myctophids, the neoscopelids, there is an A_1 present but no $A_1\beta$ (Winterbottom, 1974, Fig. 3). In addition, in the sister group of the myctophiforms plus acanthomorphs, the aulopiforms, there is also an A_1 but no $A_1\beta$ (Rosen, 1973, Figs. 27–29). The simplest explanation of this distribution is that the common ancestor of the eurypterygians had an A_1 and that within the myctophoid lineage an $A_1\beta$ is an evolutionary novelty. Similar reasoning explains the presence of a medial adductor muscle in stomiiforms and acanthomorphs.

Because the muscles termed $A_1\beta$ in neoteleosts are hypothesized to be nonhomologous, we refer to this muscle in stomiiforms simply as the medial division of the adductor mandibulae. For further discussion of adductor muscle morphology and nomenclature, see Winterbottom (1974). Lauder (1980) also comments on the medial adductor muscle in paracanthopterygians.

4) A premaxillary-rostrodermethmoid ligament extending from the dorsolateral aspect of the ethmoid to the contralateral premaxilla, or to both the contralateral and ipsilateral premaxillae (Fig. 12A, B). In some species, such as those of *Diplo-*

phos, the ligament from each side intersects and passes through that of the other side. Crossed dorsal ligaments are present in primitive members of the two major stomiiform lineages recognized by Weitzman (1974). Among these are *Neonesthes*, *Photichthys*, and *Polymetme* (Weitzman, 1974, Fig. 49) of the Photichthya, and in the Gonostomata, *Gonostoma*, *Diplophos* (Fig. 12A, B), and as figured by Weitzman (1974), *Argyripnus* (Fig. 59, as premaxillary-proethmoid ligament), *Danaphos* (Fig. 57), *Maurolicus* (Fig. 55), and *Vinciguerria* (Fig. 50). In using this character as diagnostic of the Stomiiformes, we are accepting Weitzman's (1974) evidence regarding relationships of the major lineages; alternatively, should Weitzman's groups be found invalid, the premaxillary-rostrodermethmoid ligament could be used to propose a monophyletic group composed of the above-listed genera.

We have found no other teleosts with crossed dorsal premaxillary-rostrodermethmoid ligaments like those just described. In *Galaxias* there are two broad ligamentous sheaths extending from the dorsolateral aspects of the ethmoid to the posterodorsal and posterior surfaces of the ipsilateral and contralateral premaxillae. These sheaths are much broader than the ligaments of stomiiforms and, rather than extending primarily to the borders of the premaxillae, form a broad area of attachment on the posterior surfaces of the premaxillae.

In most teleosts there are no well organized ligaments between the rostrodermethmoid (or other dorsal ethmoid elements) and the premaxillae. But suspensory ligaments from the ethmoid region to the upper jaws are present in numerous teleosts, and the patterns of such ligaments may eventually prove useful in systematic analyses; nevertheless, pending a broad comparative study, we hesitate to make any further generalizations.

5) A single, broad proximal termination of the second epibranchial which articulates with both the second and third pharyngobranchials. In other primitive teleosts the proximal termination of the epibranchial has two processes which form separate articulations with the pharyngobranchials. This character was noted by Rosen (1973: 441).

In *Diplophos* the articulation of the epibranchial with the second and third pharyngobranchials is extensive (see Figs. 10, 11). The epibranchial has a single proximal articular surface in all stomiiforms examined. Rosen (1973: 441) noted that epibranchial structure of some paralepidids is similar to that of stomiiforms; we agree with him that the similarity appears to be convergent.

6) Posterior branchiostegal abruptly larger (in a dorsoventral plane) than those more anterior. This morphology is present in most stomiiforms; in some derived species, the posterior two or three rays are abruptly larger than those more anterior (compare Fig. 9, herein, with Weitzman, 1974, Fig. 70 of *Argyripnus*).

In most other teleosts, the branchiostegals form a graded series, becoming progressively larger posteriorly. This is the case in, for example, *Hiodon*, *Elops*, *Etrumeus*, osmerids, galaxiids, salmonids, and myctophids; for a review and numerous figures of branchiostegal morphology, see McAllister (1968). An exception to the general teleostean condition is found in some acanthomorphs and a number of clupeomorph genera, in which the posterior three (or four) branchiostegals are abruptly larger than the two or three anterior (see McAllister, 1968, Pls. 9, 15, 19; Nelson, 1970, Figs. 7–9); this morphology is most parsimoniously interpreted as independently acquired in those acanthomorphs, clupeomorphs and in stomiiforms.

McAllister (1968: 48) suggested that "expansion of the upper one or two branchiostegals" characterize stomiiforms. He listed *Idiacanthus* as an exception; our specimens of that genus have the spe-

cialized branchiostegal. We do find, however, the posterior branchiostegal slender and unmodified in the malacosteid *Photostomias*, and we interpret this morphology as a secondary reduction.

7) Some branchiostegals articulating with the ventral hypohyals. This morphology is found in primitive and in most derived stomiiforms (Fig. 9). Exceptions, with branchiostegals restricted to the anterior and posterior ceratohyals, include the sternoptychids *Araiophos*, *Thorophos*, *Argyripnus*, *Sonoda*, *Polyipnus*, *Argyropelecus*, and *Sternoptyx* and the malacosteids *Aristostomias*, *Malacosteus*, and *Photostomias*. According to Weitzman's (1974) hypotheses of stomiiform and sternoptychid relationships, the lack of branchiostegals on the ventral hypohyals in these taxa is most parsimoniously interpreted as independently acquired in the *Thorophos-Araiophos* lineage, the lineage comprised of the other sternoptychid genera listed above, and in the malacosteids.

No other teleosts have been reported to have branchiostegals on the ventral hypohyals (McAllister, 1968), and we have found none.

8) Rete mirabila and associated blood vessels located at the posterior of the swimbladder, except in those specialized species which lack the swimbladder. This morphology was suggested by Marshall (1960) to be unique to "stomiatoids." In contrast, most other teleosts with retia have them anterior to or near the middle of the gasbladder, with the vascular system extending from anterior to the rete; compare gasbladder morphologies illustrated in Marshall (1960: Figs. 30, 36). In some protacanthopterygians no organized rete is present; in some mid-water oceanic protacanthopterygians, such as *Opisthoproctus*, numerous "micro-retia" are present (Marshall, 1960, Fig. 4D). Fänge (1953) illustrated swimbladder morphology and rete distributions in several phylogenetically advanced teleosts.

The only other teleosts noted by Marshall as having a posteriorly positioned rete are the berycoids *Stephanoberyx*, *Anoplogaster*, and *Melamphaes*. In these, however, the structure of the rete is more specialized and there is an oval window. In addition, other characters (see Rosen, 1973) indicate that these genera cannot be seriously considered as the sister group of stomiiforms.

The value of swimbladder morphology for diagnosing stomiiform monophyly needs to be further tested by broad comparative studies.

The characters presented above should serve to diagnose the Stomiiformes. Other authors have suggested other characters, but we have not been able to corroborate their value in our analysis. Regan's (1923) characterization of the group is inadequate because the characters either are not adequately described or are applicable at a more general level of analysis. More recently, Greenwood *et al.* (1966) considered a number of characters to be diagnostic of the "stomiatoids," including "photophores, a large basisphenoid associated with the absence of lateral prootic walls in the anterior region of the posterior myodome" (the "post-basisphenoid space" of Weitzman, 1967a), "preopercular and infraorbital lateral-line canals connected by the supraorbital canal in the frontal, often a dorsal and in some cases a ventral adipose fin, and a mesocoracoid in those members with well developed pectoral fins" (p. 372). We have discussed photophore morphology above. The "post-basisphenoid space" is present as described only in some of the more phylogenetically derived species (e.g., melanostomiatids, *Astronesthes*; see Fig. 5 of Greenwood, *et al.*, 1966 and compare with Fig. 4, herein). We were unable to find lateral-line canals as described in specimens we examined of numerous stomiiform genera. A dorsal adipose fin is a euteleostean character (Patterson and Rosen, 1977), and a ventral adipose fin is

present in only some, phylogenetically derived species, e.g., *Stomias, Chauliodus*. A mesocoracoid and a large basisphenoid are primitive for teleosts.

Monophyly and Interrelationships of the Neoteleostei

The most recent discussion of the Neoteleostei is that of Rosen (1973) (Fig. 21). He diagnosed the group on the basis of three characters (p. 505): 1) presence of a retractor arcuum branchialium muscle, RAB (called retractor dorsalis, herein); 2) presence of ascending and articular premaxillary processes (he listed this character in stomiiforms as occuring "in some members of the gonostomatid-sternoptychid complex"); and 3) presence of "an advanced type of internal maxillary muscle ($A_1\beta$)." Rosen included stomiiforms in the Subdivision Neoteleostei since they appeared to share these characters with other neoteleosts. On the basis of a number of characters, stomiiforms were considered to be the sister group (Stenopterygii) of all other Neoteleosts (Eurypterygii). The Eurypterygii was diagnosed on the basis of eight characters (these are discussed below).

Stomiiforms have in recent decades been considered related to either clupeoids or salmonoids (see Weitzman, 1967a). Greenwood *et al.* (1966) placed them within the Salmoniformes and, with the exception of Rosen's (1973) paper, this arrangement has remained the accepted one by general consensus (see Nelson, 1976; textbooks by Bond, 1979, and Lagler *et al.*, 1977).

Our own analysis of Rosen's characters and others indicates that Rosen's basic conclusions are corroborated, i.e., that stomiiforms are neoteleosts and that they are the sister group of the monophyletic Eurypterygii. We present further evidence for neoteleostean monophyly immediately below and then discuss Rosen's (1973) work on the Neoteleostei and Eurypterygii. In the next section, on protacanthopterygian relationships, we discuss our findings regarding previous hypotheses about the Salmoniformes.

Characters shared as synapomorphies by neoteleosts include the following:

1. A retractor dorsalis muscle is present. It is lacking in most non-neoteleosts (Rosen, 1973; see Winterbottom, 1974, regarding the distribution and nomenclature of this muscle and a similar one in cyprinids, gars, and *Amia*). We have confirmed the presence of the retractor dorsalis in *Diplophos*.

2. A rostral cartilage is present. The cartilage is a single median structure which lies between the premaxillae and the ethmoid region of the neurocranium. We have seen this cartilage in all major neoteleostean lineages examined, and it is illustrated several times by Rosen and Patterson (1969; see for example Figs. 15C, *Typhlichthys*; Fig. 74B, *Chloropthalmus*; Fig. 74C, *Neoscopelus*; Fig. 74E, *Myctophum*). A rostral cartilage is lacking in many phylogenetically derived stomiiforms (e.g., melanostomiatids) and in paralepidids.

Paired cartilage bodies lie anterolateral to the ethmoid region, usually between the palatine, maxilla, and ethmoid, in a number of primitive teleosts. In salmonids, paired cartilages lie along or just lateral to the midline, between the ethmoid and the premaxillae. Fusion of these cartilages would result in a body identical in form to a rostral cartilage, and it is possible that such was its origin. This possibility is considered in more detail in the discussion of protacanthopterygian interrelationships.

3. Teeth with attachment mode Type 4 (Fink, 1981). Non-neoteleosts have the primitive modes 1 and 2, with one exception noted below (see discussion of stomiiform monophyly, above, for definitions of attachment modes). Teeth with Type 4 attachment mode are hinged, with the anterior border of the tooth base

free from the underlying attachment bone, and with a relatively large unmineralized collagen area at the posterior border of the tooth base. The axis of rotation is the posterior collagen area. As discussed above in the section on stomiiform characters, and by Fink (1981), Type 4 teeth are found in juveniles of several primitive stomiiform species (including *Diplophos* and *Photichthys*), in several species with small adults, including *Pollichthys*, *Vinciguerria*, and *Valenciennellus*, and in the larger melanostomiatid *Tactostoma*. Fink (1981) found that when hinged teeth are present in aulopiforms, myctophiforms, paracanthopterygians, beryciforms, and perciforms, they have Type 4 mode of attachment.

In most adult stomiiforms, the hinged teeth are of Type 3, but the presence of Type 4 mode in juveniles of primitive stomiiforms and in adults of some other species (usually in which individuals are small) suggests that Type 4 teeth were present in the common ancestor of all neoteleosts and that the character is thus a neoteleostean synapomorphy.

The only other teleost in which Fink (1981) found Type 4 attachment mode was *Esox*. He concluded that details of morphology, combined with a lack of evidence linking *Esox* with neoteleosts, indicates that the Type 4 mode of *Esox* is independently derived.

4. The exoccipital and basioccipital bones both articulate with the vertebral column (anterior centrum and/or notochord) (Figs. 5, 7). In other teleosts examined, with two exceptions discussed below, only the basioccipital articulates with the vertebral column. The neurocranium/vertebral articulation in *Diplophos* is similar to that of other primitive stomiiforms such as *Photichthys* and *Polymetme* (the figure of the latter in Weitzman, 1967a, Fig. 13, is not accurate in that the exoccipitals should extend more posteriorly). The neurocranium/vertebral articulation is illustrated for the sternoptychid genera in Weitzman (1974). In more specialized stomiiforms, the posterior process of the exoccipital is enlarged, sometimes greatly (see Weitzman, 1967b, Figs. 5, 6, 13 for *Astronesthes*), and articulates with the thick connective tissue sheath overlying the notochord. The inclusion of both the exoccipital and basioccipital bones in the vertebral articulation was illustrated by Rosen and Patterson (1969) for aulopiforms (Figs. 61B, 63), neoscopelids (Figs. 61A, C; 63), myctophids (Fig. 61D), paracanthopterygians (Fig. 10A–D, among others), and acanthopterygians (Fig. 10E). Our own observations confirm the distribution of this character. Weitzman (1974: 360–361) has described the condition of the articulation in osmerids and stomiiforms in greater detail.

Among non-neoteleosteans we find the exoccipital included in the neurocranium/vertebral articulation in the osteoglossomorph *Hiodon* and in salmonids. In *Hiodon* the anterior vertebral centrum is firmly and closely articulated with the neurocranium; the anterior face of the centrum is convex and fits into a concavity formed by the basioccipital and exoccipital. In other osteoglossomorphs examined (*Osteoglossum*, *Arapaima*, *Scleropages*) and in notopterids (Greenwood, 1963), the articulation includes the basioccipital only. We surmise, in the context of the well documented hypothesis that osteoglossomorphs are the sister group of elopocephalans (Patterson and Rosen, 1977), that the morphology in *Hiodon* is an independent acquisition and that it may be in part related to the expansion of the exoccipitals as a part of the otophysic connection in those fishes (see Greenwood, 1973, Pl. 1).

In salmonids, the neurocranial articulation is virtually the same as that of neoteleosts, with the basioccipital and exoccipitals articulating with the anterior vertebra, and it may be that the two are sister groups. This possibility is discussed in more detail below in the section on interrelationships of protacan-

thopterygians. Should the hypothesis of this relationship be corroborated with further investigation, this character would apply to an expanded Neoteleostei (including salmonids) or to a taxon with a new name.

Two of the three character complexes used by Rosen (1973) to define the Neoteleostei appear to be invalid. These are presence of an $A_1\beta$ division of the adductor mandibulae muscle and upper jaw structure. Our opinions regarding homologies of the adductor muscles are given in the preceding section on stomiiform monophyly; we believe that the adductor muscle morphology of stomiiforms is unique to them.

Regarding upper jaw morphology, the situation is more complex. In his diagnosis of the Neoteleostei, Rosen lists presence of both ascending and articular premaxillary processes (1973: 505). However, in the text (p. 413), he also includes some other upper jaw features shared by ". . . more generalized gonostomatid and sternoptychid stomiatoids . . ." as neoteleostean features, including ". . . a low post-maxillary process on the premaxilla; a somewhat folded head on the maxilla; various ligaments extending between the palatine and ethmoid; and both upper jaw bones, in some cases, in a neoteleostean pattern (Weitzman, in press)." Some of these are easily dismissed. Weitzman (1974, cited as in press by Rosen) discussed and illustrated jaw bones in certain stomiiforms, but not those of other neoteleosts, and, as far as we know, a neoteleostean jaw bone pattern has not been defined. Presence of "various ligaments extending between the palatine and ethmoid," not defined further, is so ambiguous as to be meaningless; in fact the presence of some ligaments between the palatine and ethmoid appears to be primitive for teleosts. We find no neoteleostean palatine-ethmoid ligament pattern.

We have found articular processes (a dorsal projection of bone articulated with the maxillary head) to be common among elopocephalans, and therefore primitive for neoteleosts. No ascending process (i.e., a dorsal projection of bone medial to the articular process) has been found by us in stomiiforms. Rosen (1973) apparently interpreted the articular process in *Maurolicus* and *Neophos* (=*Thorophos* in Weitzman, 1974) as an ascending process; nevertheless, it is clear that the process in each of these examples is closely articulated with the maxilla (see Weitzman, 1974, Fig. 55 of *Maurolicus* and Fig. 51 of *Thorophos*).

We are not certain about what Rosen means when he refers to the "folded head of the maxilla." He may be referring to the morphology found in some eurypterygians wherein the proximal end of the maxilla extends dorsally over the premaxilla, or in which the maxilla is bifurcated anteriorly and extends around the ascending or articular process of the premaxilla (see, for example, Rosen and Patterson, 1969, Fig. 15 of percopsiforms). Although some stomiiforms may have an anteromedial groove in the maxilla, we have not found what we would consider a "folded head" in any stomiiform we have examined.

A post-maxillary process on the premaxilla was also considered by Rosen to be a neoteleostean synapomorphy. However, we find that such a process is absent in primitive stomiiforms, such as *Diplophos* (Fig. 4), *Polymetme* (Weitzman, 1967a, Figs. 13, 14), *Thorophos* (Weitzman, 1974, Fig. 18), and *Gonostoma*. A small bony flange extends dorsally from the premaxilla, medial to the maxilla, in *Maurolicus* (Weitzman, 1974, Fig. 22). An elongate flange also projects medial to the maxilla in *Valenciennellus* (Weitzman, 1974, Fig. 25). These latter two genera are in the Sternoptychidae, a group considered by Weitzman (1974) to be phylogenetically derived relative to the lineages represented by *Diplophos*, *Polymetme*, and *Gonostoma*. This indicates that the processes in *Maurolicus* and

Valenciennellus are specializations of those genera.

Rosen (1973) considered stomiiforms to be the sister group of other neoteleosts, the Eurypterygii (Fig. 21). The latter was considered monophyletic on the basis of eight characters (Rosen, 1973: 505–506). One character, presence of a protractor pectoralis muscle, has been found by Greenwood and Lauder (1981) to be a gnathostome synapomorphy. Two other characters should be reassessed since they both are described as "tendencies"; these are a tendency for the alveolar arm of the premaxillary to elongate and develop a post-maxillary process, and a tendency for the pectoral fins to "migrate up" on the flank and for the pelvics to move forward under the pectorals (see Introduction for discussion of evolutionary "tendencies" as characters). A fourth character, "stabilization of the ascending and articular premaxillary processes" must be assessed in view of our finding that stomiiforms have an articular process but not an ascending process. This would imply that presence of the latter character is a eurypterygian trait (see also Rosen and Patterson, 1969). Another character listed by Rosen is "development of a deeply folded articular head on the maxilla" as opposed to a "somewhat folded head on the maxilla" in stomiiforms (Rosen, 1973: 413). As noted above, eurypterygians do have a specialized maxillary morphology and this may also be a eurypterygian character; more precise descriptions are needed for further analysis.

A sixth character, an "elongate third pharyngobranchial that displaces the second pharyngobranchial from the midline . . . ," appears to diagnose two groups, the Eurypterygii and a subgroup of the Stomiiformes (Fink, in preparation). The few instances of eurypterygians with the second pharyngobranchial not displaced by the third occur in a pattern which is incongruent with current concepts of relationships within the group, so it is most parsimonious to assume that they have developed the pattern as a neomorphic feature (e.g., *Hoplostethus*, Rosen, 1973, Fig. 88).

The seventh character considered by Rosen (1973) to be a eurypterygian synapomorphy is "reduction of the second preural neural spine in the caudal skeleton to a half-spine, and the forward migration of the epurals." "Reduction" in neural spine morphology is also present in many primitive euteleosts, including esocoids (see discussion by Rosen, 1974: 292), some salmonids (e.g., *Prosopium* and *Coregonus*), and some osmerids. Whether this character is eurypterygian or applicable to a broader level of relationships is problematical, depending on assessment of relationships among the primitive euteleostean groups. At this point, however, the character does seem to diagnose the Eurypterygii. As noted by Rosen and Patterson (1969) the evolution of neural spine morphology has been complex; descriptions which clearly differentiate the various "reductive" spine morphologies for systematic purposes are not yet available. Regarding the "forward migration of the epurals" (Rosen, 1973: 506), we find no distinction between the placement of epurals in primitive eurypterygians and non-eurypterygians (compare Weitzman, 1967a, Fig. 4 of *Spirinchus*, and Rosen and Patterson, 1969, Fig. 2B of *Aulopus* with *Diplophos*, our Fig. 16).

The remaining character suggested by Rosen (1973) as diagnostic of the Eurypterygii is "a large tooth plate fused with the underside of the third epibranchial." Fusion of a toothplate to the third epibranchial is a feature which we have found only in eurypterygians and which does diagnose the group (the toothplate is lacking in ateleopodids, Rosen, 1973: 487). We would suggest that reference to tooth plate size can be eliminated, however, since in some perciforms, such as *Perca*, the tooth plate is small.

From our discussion above concerning

characters considered to be neoteleostean by Rosen, it would appear that some of them may be eurypterygian. These would include the presence of an ascending premaxillary process, a "folded head on the maxilla," and a post-maxillary process on the premaxilla. Further examination of the distributions of these characters is needed for a better assessment of them.

Lauder (1981) presents another eurypterygian character: presence of an interoperculohyoid ligament.

In summary, we agree with Rosen's (1973) hypotheses that the Neoteleostei and Eurypterygii are monophyletic and that the latter is the sister group of the Stomiiformes.

COMMENTS ON PROTACANTHOPTERYGIAN INTERRELATIONSHIPS

The traditional inclusion of stomiiforms in "basal" teleostean groups led us to examine a number of members of the various phylogenetically primitive euteleostean lineages. As noted by Rosen (1974), the Protacanthopterygii of Greenwood *et al.* (1966) has undergone steady attrition as the included groups have been placed into a more phylogenetic framework. The most recent treatment of the Protacanthopterygii (now including only the Salmoniformes) is that of Rosen (1974). We have examined the arguments for his classification within the group and present herein some discussion of his hypotheses of relationships. Rosen's (1974) contribution is examined in detail since its methodology is explicitly phylogenetic, and thus its hypotheses are ideally constructed for criticism. We make few comments on the work of other authors (e.g., Greenwood *et al.*, 1966; Weitzman, 1967a; McDowall, 1969; Gosline, 1960; Klyukanov, 1975), since none of them used explicitly phylogenetic methodology, and thus their concepts of relationship and character usage cannot be interpreted unambiguously. It is not our purpose here to provide a revision of the protacanthopterygians, but rather to present the findings that have emerged from our survey of lower teleosts, pending a more thorough survey of relationships at this level.

Rosen (1974) summarized his hypotheses concerning protacanthopterygian relationships in two places, first on page 310 and then in an "analytical" key (pp. 311–313). His hypothesis of protacanthopterygian relationships can be summarized as follows (Fig. 22). There are two major lineages. One, Infraorder Esocae, includes the Esocidae, Umbridae, and Lepidogalaxiidae; the other, Infraorder Salmonae, includes two suborders, the Argentinoidei and Salmonoidei. The Argentinoidei is comprised of the Argentinoidea and the Alepocephaloidea, and the Salmonoidei is comprised of the Salmonoidea (Salmonidae and Galaxiidae) and the Osmeroidea (Osmeridae, Plecoglossidae, Retropinnidae, and Salangidae). When formal group names are mentioned in the text below, they will correspond to Rosen's usage. When our conclusions differ from his, our use of his categories as descriptive terms follows these conventions: presumed polyphyletic groups (e.g., "salmonoids") are used with quotes, and paraphyletic groups (e.g., osmeroids) are used without quotes. The term argentinoid as used below refers to the suborder Argentinoidei, not to the superfamily Argentinoidea. Esocoid refers to members of both the Infraorder Esocae and the Esocoidei, since they are redundant categories in the classification (though only provisionally accepted herein).

Rosen's (1974: 311–314) "analytical key" is ambiguous about which characters were used as synapomorphies for which groups. For most of the characters both the derived and primitive states are given in a single couplet; thus the derived state is synapomorphic at some lower taxonomic level and not diagnostic

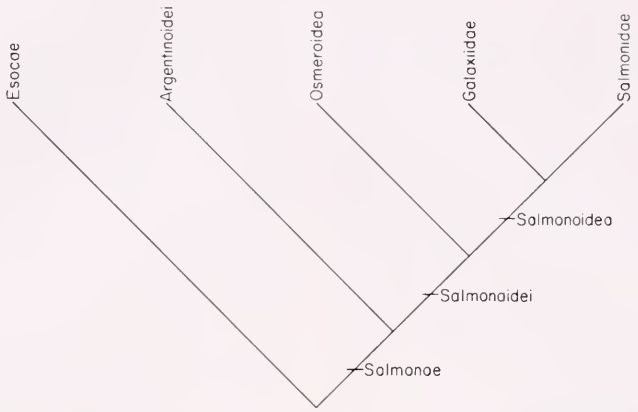

Figure 22. Rosen's (1974) hypothesis of choice for protacanthopterygian relationships.

of the group that "keys out" at that couplet. In some cases, characters were used as synapomorphies at several levels in the key, without explanation. In spite of the confusing structure of the key, a careful reading of it, combined with a reading of the text, does provide some characters which appear to be diagnostic of the various groups recognized by Rosen.

Our discussion of Rosen's hypotheses follows the sequence of taxa as given in his key, which the reader may wish to consult.

The Protacanthopterygii was never explicitly diagnosed by Rosen, but the characters which he suggested to unite esocoids (including *Lepidogalaxias*) with the other lineages can be construed as protacanthopterygian synapomorphies. These characters were discussed on page 310 and include fusion of a toothplate (when present) to the third pharyngobranchial and presence of "a posterior toothplate below the fourth pharyngobranchial and fourth epibranchial in a pattern like that of the 'well toothed' salmoniforms." However, the first of these characters is probably clupeocephalan, since fusion of the toothplate occurs not only in salmoniforms but also in *Etrumeus*, ostariophysans, stomiiforms, and almost all eurypterygians (with the exception of the Ateleopodidae, noted by Rosen, 1973: 487). Concerning the second character, Rosen did not precisely define the pharyngobranchial toothplate "pattern" or "well toothed," but we assume that he is referring to the presence of but a single toothplate associated with the fourth pharyngobranchial and fourth epibranchial. This character has a distribution in the Protacanthopterygii which indicates that convergence is common. There are two toothplates in this position in argentinoids we examined, in galaxiids (see Rosen, 1974, Fig. 11b, c), and in some osmeroids (see Rosen, 1974, Fig. 12b). It would appear that the fusion (or loss) of the toothplate on the fourth pharyngobranchial has occurred in salmonids, some osmeroids, and esocoids, and that the character cannot be definitive for the Protacanthopterygii. Rosen admits that the evidence for inclusion of esocoids in the group is "slight," and we agree.

Of the eleven characters Rosen (1974) used to place *Lepidogalaxias* in the Esocae, only four appear to be appropriate for inference of relationship between those groups: lack of a mesocoracoid, lack of pyloric caeca, a single rudimentary neural arch and spine over PU1, and a single uroneural. In view of the reductive

nature of all of these characters and the very small size and benthic "habits" of *Lepidogalaxias*, and in view of the importance of the biogeographic hypothesis suggested by this hypothesis of relationships, it appears to us that a further search for characters is warranted. This is especially so since in the original description of *Lepidogalaxias*, Mees (1961: 33) states that there is a single series of comparatively large teeth on the entopterygoids (mesopterygoids, herein), a character which we propose below to be a synapomorphy for osmeroids (including galaxiids); Rosen (1974) states that *Lepidogalaxias* lacks teeth on the bone. This contradictory evidence needs to be reexamined.

Of the thirteen characters listed in Rosen's key as diagnostic of the Infraorder Salmonae, only one appears to represent a possible synapomorphy: lack of a toothplate on the fourth endoskeletal basibranchial. Rosen's text (1974: 237) would appear to contradict the utility of this character, since he reports the toothplate in *Retropinna* and *Osmerus*, both members of the Salmonae. While we have not found the toothplate in specimens of those genera available to us, we nevertheless doubt the utility of the character as diagnostic of the Salmonae since the toothplate is also lacking in other primitive euteleosts, including ostariophysans (except the phylogenetically derived characiform *Prochilodus* and, according to Rosen, the characiform *Ichthyborus* [1974: 273]), stomiiforms and aulopiforms. Dentigerous toothplates are present on the fourth basibranchial of *Elops*, *Megalops*, *Hiodon*, and *Chirocentrus* (but lacking in all other clupeomorphs). This distribution pattern suggests to us that the Esocae, whose members have the toothplate, may be the sister group to all other euteleosts (the toothplate is also reported in *Lepidogalaxias* by Rosen, 1974).

Two additional characters of the Salmonae are listed in Rosen's text (p. 310): presence of fanglike teeth arranged marginally on the basihyal and development of platelike bone on the posterior neural and hemal spines. Interpretations of the term "fanglike" will vary with each investigator, and we find a morphological continuum from "large fanglike" to "small fanglike" to "teeth along the lateral basihyal border somewhat larger than those on the medial surface of the bone." These definitions are of necessity highly subjective and are best understood by an examination of actual specimens. Large, fanglike, and usually recurved teeth, proportionally much larger than teeth found in other primitive euteleosts, are found in salmonins (e.g., *Cristivomer*, *Salvelinus*, *Salmo*, *Oncorhynchus* [Rosen, 1974, Fig. 3A–E, respectively], and *Brachymystax*), and in the osmerid *Spirinchus*. In *Osmerus* large "fanglike" teeth are present around the anterior region of the basihyal, but the more posterior teeth are all much smaller, and those along the border are about equal in size to those on the medial portion of the bone. Teeth which are "fanglike" and recurved but not large are found in galaxiids, *Retropinna*, and *Argentina*. Genera in which the marginal basihyal teeth are somewhat larger than those on the rest of the bone include the osmerids *Hypomesus* and *Mallotus* (Rosen, 1974, Fig. 2A, B) and our specimens of *Plecoglossus*; Rosen's figure of *Plecoglossus* (2C) shows a scattering of larger teeth among some smaller teeth. We found that basihyal teeth in *Prosopium* (Rosen, 1974, Fig. 3F) and *Thymallus* to be uniformly small. Basihyal teeth are either small in both size and number or not present in most argentinoids (Greenwood and Rosen, 1971).

This cursory and incomplete survey of basihyal tooth morphology indicates to us that presence of enlarged marginal basihyal teeth would be diagnostic of the Salmonae, if the presence of small teeth in some salmonids and argentinoids is found to be a secondary reductive fea-

ture. This can only be assessed in the context both of more characters and of hypotheses of phylogenetic relationships within the various protacanthopterygian groups.

Platelike bone on the neural and hemal spines, the second character of the Salmonae listed in Rosen's text, is well developed in many members of the group (see Rosen, 1974, Figs. 18, 19, 25–27; Gosline, 1960). We find use of this character difficult because of our uncertainty about what Rosen intended by "platelike." In many members of the Salmonae there is extensive laminar bone on the neural and hemal spines, forming large blade-like structures (see Rosen, 1974, Figs. 18A, *Galaxias vulgaris*; 25B, *Salmo*; 26C, *Plecoglossus*; 27D, *Retropinna*). In other members of the group, the lamellar bone is less extensive, often forming ovoid anterior extensions from the spines (see Greenwood and Rosen, 1971, Figs. 11B, *Searsia*; 12B, *Glossanodon*; 14, *Bathylagus*; 16A, *Osmerus*). In yet others, there is very little or no lamellar bone on the spines (see Greenwood and Rosen, 1971, Figs. 8, *Talismania*; 10, *Rouleina*; Rosen, 1974, Fig. 19, *Aplochiton*; Weitzman, 1967a, Fig. 4, *Spirinchus*). In *Cristivomer*, the neural spines have little lamellar bone, while on the hemal spines it is more extensive. In primitive teleosts generally, some lamellar bone on the neural and hemal spines in the caudal region is common, e.g., in *Elops*, *Denticeps*, many characiforms, and *Aulopus* (it is extensive and blade-like in the latter). Nevertheless, it could be argued that some amount of elaboration of lamellar bone is a diagnostic character of the Salmonae and that its absence in some members of the group (e.g., alepocephaloids, *Spirinchus*) is a secondary loss. We would like to see a more precise definition of the character, however, than that provided by Rosen (1974).

Rosen (1974) diagnosed the suborder Argentinoidei on the basis of three unique characters: basibranchial toothplate with a sharp ridge of bone and a membrane that divides the orobranchial chamber into right and left halves, presence of a crumenal organ, and accessory cartilage at the posterior end of the fifth ceratobranchial; see also Greenwood and Rosen (1971).

The suborder Salmonoidei is undefined by the characters presented by Rosen (1974).

The superfamily Salmonoidea (Salmonidae and Galaxiidae, including Aplochitoninae) is diagnosed by Rosen by the presence of paired marginal basihyal teeth, none or few scattered teeth on the basibranchials, and the fourth epibranchial without uncinate or levator processes. Paired basihyal teeth, rather than alternating teeth with a single tooth at the anterior apex of the bone, are found in most salmonids and many specimens of galaxiids. However, about half of the galaxiids we examined have a single terminal tooth and alternating tooth pairs along the basihyal margin. In addition, some osmeroids approach the "paired" tooth condition (see, e.g., Fig. 4A, C of Rosen, 1974). Lack of teeth or presence of a few scattered teeth on the basibranchials is a character present also in argentinoids and stomiiforms. Lack of an uncinate process on the fourth epibranchial is not a feature common to all galaxiids; our specimens of both *Galaxias anomalous* and *G. delfini* have such a process. Loss of the uncinate process appears therefore to be independent in salmonids and galaxiids. Absence of a "levator process" is a character which, as defined, may lead to confusion. In teleosts generally a levator muscle attaches to the dorsolateral surface of the fourth epibranchial (Winterbottom, 1974). In many primitive euteleosts, this surface is separated from the ventrolateral extremity of the bone by a concavity, so that the area of levator insertion may be termed a process. Rosen's character, "absence of a levator process," might better be defined as loss of this concavity; the area of levator attachment

remains unchanged, although in descriptive terms it is no longer a process. Absence of this concavity is a feature shared not only by salmonids and galaxiids, but also by the osmeroids *Stokelia*, *Retropinna*, *Salangichthys*, and by esocoids, except *Umbra*.

Thus, of the four features suggested by Rosen to be synapomorphies for his Salmonoidea, two (paired basihyal teeth and no uncinate process) are not always present in galaxiids, one (reduced basibranchial dentition) is shared also with argentinoids (and stomiiforms), and the other (no distal concavity in the epibranchial) is shared with esocoids and some osmeroids. We would prefer a search for other characters to substantiate monophyly of the Salmonoidea, particularly since we have found evidence, presented below, which suggests other relationships for both the galaxiids and the salmonids.

The Osmeroidea (including Salangidae, Osmeridae, Plecoglossidae and Retropinnidae), is diagnosed in Rosen's key by two characters which appear to represent possible synapomorphies. These are the presence of a blunt, somewhat elevated median ridge on the second basibranchial toothplate, except when the toothplate is greatly expanded, and lack of autogenous rudimentary neural arches dorsal to PU1, these arches having become fused into a dorsal outgrowth of the first uroneural. In the osmeroids examined by us (*Osmerus*, *Mallotus*, *Spirinchus*, *Hypomesus*, *Retropinna*), the basibranchial toothplate is smoothly, though fairly steeply, arched dorsally along most or all of its length. No blunt median ridge is present. The basibranchial toothplate is similarly shaped in *Elops*, *Megalops*, *Chirocentrus*, *Aulopus*, and *Neoscopelus*, and would appear therefore to be primitive in form in osmeroids. The second osmeroid character of Rosen (1974: 313) is the presence of a "stegural," defined as a complex formed by fusion of the rudimentary neural arch(es) of PU1 to the first uroneural (see also Greenwood and Rosen, 1971). Rosen contrasted this condition with that of salmonids, wherein the rudimentary neural arches "join" but do not fuse with the uroneural, forming a "primitive stegural" (Patterson and Rosen, 1977: 122–126, have recently redefined the term stegural, so we enclose the "stegural" of Rosen, 1974, in quotation marks). Our observations confirm that adult osmeroids do have the rudimentary neural arches fused to the first uroneural, and that this appears to be part of an ontogenetic sequence, since in our smaller specimens the arches are not yet fully fused with the uroneural (see Rosen, 1974, Fig. 28). We have observed the bones to be fused in adults of *Retropinna*, *Mallotus*, *Spirinchus*, *Hypomesus*, and *Osmerus*. Some osmeroids also have the rudimentary neural arches fused with PU1, but such fusion apparently occurs later in ontogeny than fusion to the uroneural; a large (154 mm SL) specimen of *Osmerus* (MCZ 56535) has two large rudimentary neural arches over PU1 and fused with both the uroneural and the centrum. Fusion of rudimentary neural arches to both the uroneural and PU1 are found in some argentinoids and galaxiids also, but in these fishes fusion to the uroneural appears to occur later in ontogeny than fusion to PU1. Most of the galaxiids examined by us are small specimens and have the arch(es) fused with the centrum but not the uroneural; however, in a 238 mm SL specimen of *Galaxias delfini* (MCZ 46284) there are two rudimentary neural arches fully fused with both the centrum and the uroneural. Two small specimens (44 mm and 71 mm SL) from the same collection as that specimen have the arches unfused with the uroneural. Rosen noted fusion of the neural arches to the uroneural in some galaxiid specimens (1974: 296, Figs. 18E of *Galaxias maculatus*, 19B of *Aplochiton taeniatus*, 19C of *Lovettia seali*), but he did not indicate sizes of the specimens he examined.

To summarize our observations on rudimentary neural arch/uroneural fusion patterns, there appear to be two fusion patterns of these bones in protacanthopterygians. In argentinoids and galaxiids, when fusion takes place, the arches fuse first with the centrum and then with the uroneural. In osmeroids, the arches fuse first with the uroneural and then, in some cases, with the centrum. Salmonids, many argentinoids, and esocoids do not have uroneural/rudimentary neural arch fusion. The phylogenetic significance of the two fusion patterns is unclear at present, and a decision as to whether they suggest that argentinoids and galaxiids are sister groups and that osmeroids are monophyletic, or whether the fusion pattern of either of these two "groups" is primitive, must await more detailed analysis and comparisons in the context of other characters.

In addition to the various protacanthopterygian characters listed above, fusion of the fifth epibranchial to the fourth was discussed in detail by Rosen (1974: 284, Figs. 8–10, 14, 16). He considered fusion between the dorsal tip of the fifth epibranchial and the midpoint of the dorsolateral border of the fourth epibranchial to be an additional derived character for the Salmonoidea (Salmonidae plus Galaxiidae). Similarly, a fusion of the ventral tip of the fifth epibranchial to the posteroventral end of the fourth was considered derived for the Osmeroidea. However, Rosen found fused epibranchials only in one salmonid, *Prosopium*, and in some osmeroids there was no fusion. Use of these fusions as characters at the "salmonoid" and osmeroid levels presumes loss of fusion in some members of each group. Such a presumption appears unwarranted at this time, since the current lack of information on both osmeroid and salmonid phylogeny precludes a parsimony assessment.

As should be evident from our survey of the most recent presentation of evidence regarding protacanthopterygian relationships, we think that alternative hypotheses should be considered. A full analysis of protacanthopterygian interrelationships is beyond the scope of this paper, but we interpret below some morphological evidence examined during the course of this study; our hypotheses of relationship are illustrated in Figure 23.

Several features were found which might be synapomorphous for a group consisting of osmeroids and galaxiids (*sensu* Rosen, 1974) and thus supportive of previous workers' conjectures (Gosline, 1960; McDowall, 1969). First, in members of both groups there is a series of large teeth along the medial border of the mesopterygoid (in some osmeroids, such as *Retropinna* and *Plecoglossus*, there are also some smaller teeth lateral to the large serial teeth). In most primitive teleosts with mesopterygoid teeth, including *Elops*, *Megalops*, *Etrumeus*, and *Diplophos*, the teeth are small and scattered over the ventral surface of the bone. Large, serially arranged mesopterygoid teeth are present in *Scleropages* and *Osteoglossum*, but the evidence that these osteoglossomorphs are phylogenetically distant from osmeroids is quite strong (Patterson and Rosen, 1977) and the similarity is considered by us to be convergent.

We suggest that in osmeroids and galaxiids there is a specialized "tongue bite" mechanism in which food is manipulated between the basihyal teeth and the mesopterygoid teeth. This would parallel the "tongue bite" in the osteoglossomorphs mentioned above. In some salmonids, including *Salmo* and *Oncorhynchus*, there is also a morphology which appears to be a "tongue bite" mechanism, but in these fishes the dorsal teeth lie on the greatly elongated vomer and the mesopterygoid is toothless (as in all salmonids).

A second feature shared by osmeroids and galaxiids is the lack of a basisphenoid bone, apparently a derived condition.

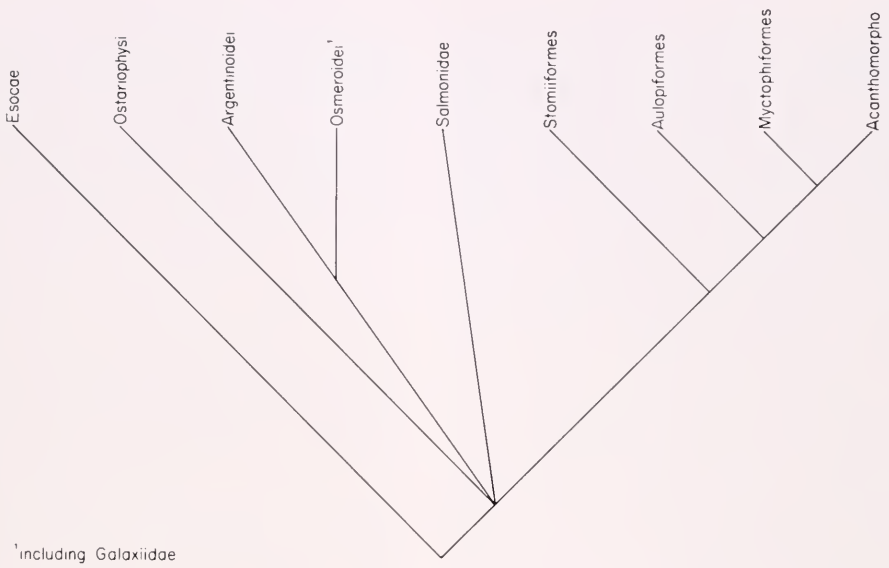

Figure 23. Summary cladogram of the hypotheses suggested from our survey of primitive euteleostean groups. Relationships of aulopiforms, myctophiforms, and acanthomorphs from Rosen, 1973.

This bone is present in most primitive teleosts, including esocoids, argentinoids, salmonids, and stomiiforms. A basisphenoid is not present in ostariophysans (Fink and Fink, 1981).

Third, osmeroids and galaxiids also lack an orbitosphenoid bone. An orbitosphenoid is present in most primitive teleosts, but is also lacking in the salmonid *Thymallus* (Norden, 1961), in some species of *Coregonus* (Norden, 1961), and in stomiiforms.

The presence of large, serially arranged mesopterygoid teeth in osmeroids and galaxiids, unique within the elopocephalans, together with the absence of orbitosphenoid and basisphenoid bones, supports the placement of galaxiids within the osmeroid assemblage. Rosen listed all family level groups in the Osmeroidea as *incertae sedis*; we would add to that list the Galaxiidae, pending further work. The possibility of relationship of *Lepidogalaxias* to the osmeroids has been noted above, based on the presence of serially arranged teeth on the mesopterygoid; the two authors who have examined this fish (Mees, 1961 and Rosen, 1974) disagree on whether those teeth are present.

Two features suggest that the salmonids may be more closely related to the neoteleosts than to the rest of the "protacanthopterygians." The first of these is the configuration of the posterior neurocranium and the articulation of the skull with the anterior vertebra. In salmonids, the exoccipital as well as the basioccipital articulates with the anterior vertebra. In *Brachymystax* and *Thymallus* (see Norden, 1961, Pl. 2 for *Thymallus*), exoccipital/basioccipital morphology is much as in *Diplophos*. In almost all non-neoteleostean and non-salmonid teleosts we examined, only the basioccipital articulates with the anterior vertebra. The only exception is *Hiodon*; as discussed above in the section on stomiiform relationships, the morphology of the articulation is quite different in *Hiodon* and the inclusion of the exoccipital in the joint seems clearly to be convergent.

The second feature is the presence of a cartilage structure between the ethmoid and the premaxillae. We have noted in the section on Relationships of the Stomiiformes that a rostral cartilage is a neoteleostean feature. This single, median cartilage body lies between the ethmoid and the premaxillae (see Fig. 4). In a number of primitive teleosts there is a pair of cartilage bodies or ossifications which articulate between the ethmoid, palatine, and, often, the maxilla of each side. Patterson and Rosen (1977) term a large, tightly articulated ossification in this position the ethmopalatine and note that smaller but possibly homologous elements are present in esocoids, cyprinoids (=Cypriniformes, *sensu* Fink and Fink, 1981), mormyroids and notopterids. Fink and Fink (1981) have also found them in *Chanos* and some characiforms. We have observed paired cartilage bodies in several salmonids also, but they lie in a unique configuration strongly suggestive of the rostral cartilage. The cartilages lie anterior rather than lateral to the ethmoid, near or along the midline, and are attached to the premaxillae. Among the fishes we examined, the largest of these bodies were found in *Prosopium*; in this fish they are paired blocks which meet at the midline.

It is our suggestion that basioccipital/exoccipital morphology, described above, and the presence of medial cartilage bodies between the ethmoid region and the premaxillae, both provide evidence for a realignment of the salmonid fishes as the sister group of the Neoteleostei. Evidence for relationship of the salmonids with argentinoids and osmeroids (including galaxiids) consists of the presence of enlarged teeth along the margin of the basihyal and platelike bone on some neural and hemal spines.

In summary of this section, we have surveyed the morphology of teleosts previously considered closely related to stomiiforms, primarily using Rosen's (1974) analysis of relationships of the "protacanthopterygian" groups. A thorough morphological study will be needed to test Rosen's hypotheses in detail, but we have found some evidence in the course of the current study which may aid in setting the directions for future research. First, we are unable to conclude that the Protacanthopterygii is a monophyletic group. Esocoids seem to share no unique specializations with the other included taxa; we could list esocoids as *sedis mutabilis* at the euteleostean level or as the sister group of all other euteleosts, depending on placement of the ostariophysans. Second, we have expressed some reservation about inclusion of *Lepidogalaxias* with the esocoids. Third, we have doubts about a hypothesis of monophyly of the Argentinoidei plus Salmonoidei plus Osmeroidei (Infraorder Salmonae) and have discussed the three characters which may diagnose the group. Fourth, we agree with Greenwood and Rosen (1971) on the monophyly of the Argentinoidei, as diagnosed by them. Fifth, no features have yet been suggested to support the proposed hypothesis of relationship among the osmeroids, salmonids, and galaxiids. We agree with Rosen's placement of retropinnids (*Retropinna*, *Stokelia*, and *Prototroctes*), plecoglossids, salangids and osmeroids as unresolved sister taxa, but we would add to that group (Rosen's Osmeroidei) the Galaxiidae (Galaxiinae and Aplochitoninae). And, finally, we have found some characters which can be interpreted as suggesting a sister group relationship between salmonids and neoteleosts.

The Ostariophysi, a major primitive euteleostean lineage, has not been dealt with in detail since the group historically has never been considered relevant to stomiiform relationships and we have found no evidence to suggest that it is. Lack of a toothplate over the fourth basibranchial is a character ostariophysans share with all non-esocoid euteleosts. In-

terrelationships of the major ostariophysan lineages have been recently analyzed by Fink and Fink (1981).

This much is clear from our survey of the "basal" euteleosts—much work remains to be done before we have a stable hypothesis of the relationships of these major phylogenetic lineages.

SUMMARY

1. Two of the species of *Diplophos*, *D. maderensis* and *D. taenia*, are described osteologically. Certain muscles and other parts of the soft anatomy are also described.

2. Monophyly of the Stomiiformes is documented by eight synapomorphic characters, including: 1) photophore morphology, 2) Type 3 tooth attachment mode, 3) a particular subdivision of the adductor mandibulae muscle, 4) rostrodermethmoid-premaxilla ligament extending from the ethmoid to the contralateral (and sometimes also the ipsilateral) premaxilla, 5) a single, broad, proximal termination of the second epibranchial which articulates with both the second and third pharyngobranchials, 6) posterior branchiostegal abruptly larger than those more anterior, 7) some branchiostegals articulating on the ventral hypohyals, and 8) rete mirabila and associated blood vessels located at the posterior of the swimbladder.

3. Monophyly of the Neoteleostei is documented by four synapomorphic characters, including: 1) a retractor dorsalis muscle, 2) a rostral cartilage, 3) Type 4 tooth attachment mode, and 4) exoccipital and basioccipital bones both articulating with the vertebral column.

4. Monophyly of the Eurypterygii is discussed in the context of Rosen's (1973) analysis; the group is tentatively accepted as natural, primarily diagnosable by presence of a toothplate fused with the third epibranchal.

5. The primitive teleostean group Protacanthopterygii, most recently defined (Rosen, 1974) (see Fig. 22) to include the Esocoidei, Argentinoidei, and Salmonoidei (including the Salmonoidea and Osmeroidea) may be an artificial assemblage. We find no evidence to consider esocoids closely related to the other members of the group. The Argentinoidei plus Salmonoidei may be monophyletic, based primarily on presence of enlarged teeth along the margin of the basihyal, but there is also evidence which suggests that the Salmonoidei is not monophyletic and that salmonids may be the sister group of the Neoteleostei. Galaxiids (including the Aplochitoninae) are considered to be osmeroids, rather than "salmonoids" as proposed by Rosen (1974). Our alternative hypothesis of relationships of the "basal" euteleosts is summarized in Figure 23.

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APPENDIX

Material examined, listed by family. Within a family, genera are listed alphabetically. For specimens which were cleared and stained, we include number of specimens examined, their standard lengths, and "CS." Specimens which were dissected are noted by "D"; skeletons are designated by SK. Specimens which were examined externally only are listed simply by museum number. Museum acronyms are DANA (Carlsberg Foundation Dana Collections), ISH (Institut fur Seefisherei, Hamburg), MCZ (Museum of Comparative Zoology, Harvard University), SU (Stanford University, collection now housed at the California Academy of Sciences, San Francisco), and USNM (National Museum of Natural History, Washington, D.C).

TAXON	MUSEUM NO.	NO.	SIZE (mm)	PROC.
Osteoglossidae				
Scleropages sp.	MCZ 54924	1	61.6	CS
Hiodontidae				
Hiodon tergisus	USNM 167970	2	70–72	CS
Elopidae				
Elops saurus	USNM 128290	2	67.0–111.2	CS
Megalopidae				
Megalops cyprinoides	USNM 199836	2	68.0–73.0	CS
Denticipitidae				
Denticeps clupeoides	USNM 195992	1	DAMAGED	CS
Denticeps clupeoides	MCZ 56428	1	32.6	CS
Chirocentridae				
Chirocentrus dorab	MCZ 41825	2	DAMAGED	CS
Clupeidae				
Dorosoma smithi	USNM 225024	1	56.2	CS
Etrumeus sadinia	USNM 188950	2	80–81	CS
Umbridae				
Dallia pectoralis	USNM 111643	1	112.8	CS
Umbra limi	USNM 193184	1	58.7	CS
Esocidae				
Esox niger	MCZ 56945	2	91.1–94.0	CS
Argentinidae				
Argentina striata	USNM 188224	2	112–125	CS
Glossanodon struhsakeri	USNM 36418	1	117.0	CS
Bathylagidae				
Bathylagus ochotensis	USNM 199826	1	DAMAGED	CS
Salmonidae				
Brachymystax lenok	USNM 105110	1	112	CS
Coregonus stanleyi	MCZ 52007	1	146	D,CS
Coregonus sp.	MCZ uncat.	1		SK
Coregonus sp.	MCZ uncat.	1		SK
Cristivomer namaycush	MCZ 52577	1	131	CS
Hucho hucho	MCZ 7003			
Prosopium coulteri	USNM 102375	2	84.8–88.2	CS
Salmo gairdneri	CAS(SU) 49265	4	68–72	CS
Thymallus arcticus	MCZ 32362			
Osmeridae				
Hypomesus pretiosus	MCZ 32720	1	156.0	CS
Hypomesus pretiosus	USNM 10472	4	92–116	CS
Mallotus villosus	USNM 130301	3	87.8–104.7	CS
Mallotus villosus	MCZ 39849			
Osmerus mordax	MCZ 56535	1	154.0	CS
Osmerus mordax	MCZ 57013	2	40.5–58.1	CS
Spirinchus thaleichthus	MCZ 104689	2	108.5–115.6	CS
Plecoglossidae				
Plecoglossus altivelis	MCZ 4014			
Plecoglossus altivelis	MCZ 29028			

APPENDIX. Continued.

Retropinnidae				
Prototroctes muraena	MCZ 6867			
Retropinna retropinna	USNM 201161	1	78.9	CS
Salangidae				
Salanx microdon	MCZ 25485			
Galaxiidae				
Aplochiton zebra	MCZ 46272			
Brachygalaxias bullocki	MCZ 46306	21	25–30	CS
Galaxias maculatus	MCZ 46301	20	45–65	CS
Galaxias anomalus	MCZ 46293	14	25–57	CS
Galaxias delfini	MCZ 46284	2	44–71	CS
		1		D
Gonostomatidae				
Cyclothone pallida	MCZ 56961	2		D
Diplophos greyae	USNM 135691	1	105.8	CS,part
Diplophos maderensis	MCZ 54303	1	110	CS
Diplophos maderensis	MCZ 56952	1		D
Diplophos maderensis	USNM 186282	1	111.5	CS
Diplophos rebainsi	USNM 225012	1	252.0	CS,part
Diplophos rebainsi	ISH 543-76	1		
Diplophos rebainsi	ISH 73-76	1		
Diplophos taenia	MCZ 54302	1	184.3	CS
Diplophos taenia	MCZ 52536	1		D
Diplophos taenia	MCZ 52569	1		D
Diplophos taenia	MCZ 52548	3	34.0–62.0	CS
Diplophos taenia	MCZ 55469	1		D
Diplophos taenia	USNM 206614	1	171.0	CS
Gonostoma elongatum	MCZ 53133		233.0	CS
Gonostoma elongatum	MCZ 56964	1		D
Margrethia obtusirostra	MCZ 56967	1		D
Triplophos hemingi	USNM 199832	1	175	CS
Sternoptychidae				
Argyropelecus lychnus	MCZ 56948	1		D
Argyropelecus olfersi	MCZ 56969	1		D
Maurolicus muelleri	MCZ 56949	1		D
Polyipnus polli	MCZ 56965	1		D
Photichthya*				
Aristostomias grimaldii	MCZ 57014	1	140.0	CS
Astronesthes sp.	MCZ 56951	1		D
Astronesthes gemmifer	MCZ 42864	1		D
Astronesthes lucifer	USNM 225046	1	141.8	CS
Chauliodus schmidti	USNM 225045	4	51.2–165.0	CS
Echiostoma sp.	USNM 199839	2	264.7–275.7	CS
Heterophotus ophistoma	USNM 225025	2	133.2	CS
Ichthyococcus irregularis	USNM 201385	1	39.5	CS
Idiacanthus fasciola	DANA 3784-VIII	1	323.3	CS
Idiacanthus fasciola	MCZ 57012	1	470.0	CS
Macrostomias longibarbatus	USNM 225035	1	205.5	CS
Malacosteus niger	MCZ 53286		124.1	CS
Melanostomias cf. *biseriatus*	USNM 199847	1	193.5	CS
Melanostomias sp.	MCZ 56955	1		D
Neonesthes capensis	USNM 199823	1	114.1	CS
Photichthys argenteus	MCZ 56953	1		D
Photichthys argenteus	MCZ 56950	1		D
Photichthys argenteus	USNM 203407		93.1	CS
Photonectes margarita	MCZ 57010	1	159.0	CS

* Infraorder, not divided into families.

APPENDIX. Continued.

Photostomias guernei	USNM 225027	1	127.2	CS
Pollichthys mauli	USNM 201278	2	32.5–35.0	CS
Pollichthys mauli	MCZ 56954	1		D
Polymetme corytheola	MCZ 56968	1		D
Polymetme corytheola	MCZ 40918	1		D
Polymetme corytheola	USNM 199507	1	174.0	CS
Polymetme corytheola	USNM 225166	1		D
Rhadinesthes decimus	USNM 225044	1	325.0	CS
Stomias boa	MCZ 53384	1	225	CS
Tactostoma macropus	MCZ 57011	1	168.0	CS
Tactostoma macropus	USNM 187654	1	124.4	CS
Trigonolampa miriceps	USNM 206683	1	166.9	CS
Vinciguerria lucetia	USNM 201315	12	17.0–47.6	CS
Woodsia nonsuchae	MCZ 49083	1		D
Aulopidae				
Aulopus filamentosus	USNM 225043	2	143–173	CS,D
Aulopus nanae	MCZ 40516	1		D
Bathysauridae				
Bathysauris mollis	MCZ 40518	1		D
Chloropthalmidae				
Chloropthalmus agassizii	MCZ 40539	1		D
Chloropthalmus agassizii	USNM 159377	1	121	CS
Synodontidae				
Synodus intermedius	MCZ 46617	1	123	CS
		1		D
Paralepididae				
Paralepis elongata	MCZ 43129	1	129	CS
Neoscopelidae				
Neoscopelus macrolepidotus	MCZ 35596	1		D
Neoscopelus macrolepidotus	USNM 188056	2	116–117	CS,D
Myctophidae				
Lampanyctus iselinoides	MCZ 52900	1		D
Lampanyctus tenuiformis	MCZ 56963	1		D
Lepidophanes guentheri	MCZ 56960	1		D
Myctophum affine	MCZ 56947	2	62.6–70.0	CS
Myctophum asperum	MCZ 56966	1		D
Notoscopelus kroyeri	MCZ 55532	1		D
Taaningichthys bathyphilus	MCZ 53796	1		D
Talismania homoptera	MCZ 51959	1		D
Triphoturus mexicanus	MCZ 56962	1		D
Percopsidae				
Percopsis omiscomaycus	MCZ 41221	1	56	CS
Apogonidae				
Synagrops microcephalus	MCZ 56946	1	54.3	CS
Percidae				
Perca flavescens	MCZ 48920	1	68.4	CS
Coryphaenidae				
Coryphaena hippurus	MCZ 56944	1	69.5	CS

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THE EVOLUTION AND INTERRELATIONSHIPS OF THE ACTINOPTERYGIAN FISHES

GEORGE V. LAUDER[1] and KAREL F. LIEM[2]

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ABSTRACT. The phylogenetic relationships of ray-finned fishes are critically reviewed, and major features in the evolution of actinopterygian fishes are discussed and summarized. Significant progress has been made over the last fifteen years in defining the interrelationships of ray-finned fishes, but much of this progress has not been widely noted, especially by experimental biologists. Several currently accepted higher taxa are only poorly defined (e.g., the Acanthopterygii) while others are not corroborated by any uniquely derived features (the Protacanthopterygii and Paracanthopterygii). These taxa exemplify areas in need of reexamination by systematic ichthyologists.

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INTRODUCTION

The ray-finned fishes comprising the subclass Actinopterygii form by far the most diverse group of vertebrates. With almost 23,000 species of actinopterygian fishes known, they total more than half of all extant vertebrate species and have diversified to an extent unparalleled within the chordates. This tremendous radiation has resulted in extensive variation not only in morphology but also in behavior and ecology, and members of the most advanced group of actinopterygians, the Teleostei, have penetrated virtually every conceivable habitat and range from the ocean depths (−11,000 m) to high mountain streams (+4,500 m) and from hot springs (43° C) to subfreezing water (−1.8° C) (Lagler *et al.*, 1977; J. Nelson, 1976; Somero and De Vries, 1967). Teleosts also contain the smallest adult vertebrates, with one species becoming adult at 7.5 mm or less (Miller, 1979). While this diversity has provided fertile ground for comparative studies on actinopterygian anatomy, behavior, and ecology, it has also compounded the problems faced by systematic ichthyologists in unravelling the interrelationships and evolutionary history of the actinopterygian fishes. In the last fifteen years, and especially since the monograph by Greenwood *et al.* (1966), considerable progress has been made in determining the relationships between the various major groups of ray-finned

fishes. The primary goals of this review will be to summarize the recent advances in phylogenetic reconstruction, present these data in a form that will be of use to ichthyologists, vertebrate paleontologists, and comparative and experimental biologists in general, and to integrate major recent discoveries in functional morphology into a phylogenetic context. The lack of a current critical review of progress and problems in the analysis of actinopterygian evolution has stimulated this paper. We have not attempted an exhaustive survey of the literature on actinopterygian fishes, nor have we solved many of the current problems in fish phylogenetics. Rather, we highlight those areas most in need of further work, and rely heavily, but not exclusively, on the literature for characters supporting monophyly of the major actinopterygian subgroups. In providing a general critical review, we hope to clearly define the areas in which current data are inadequate to support both hypotheses of relationship and functional evolutionary scenarios, as well as to contribute new ideas and suggestions for resolving problems of pattern and process in actinopterygian evolution.

Recent advances in deciphering actinopterygian phylogenetic patterns have been primarily achieved by applying the principles of phylogeny construction formulated by Hennig (1966). (More recent summaries of genealogical methodology may be found in Eldredge and Cracraft, 1980; Gaffney, 1979; Wiley, 1975, 1976.) In presenting a review of actinopterygian relationships and biology, then, we will emphasize monophyletic assemblages of taxa (*sensu* Hennig) defined as follows: a monophyletic taxon is a group stemming from a single common ancestor and containing all known descendants of that ancestor. In recent years, systematic ichthyologists have increasingly regarded monophyletic lineages as representing natural evolutionary units, and have attempted to identify monophyletic taxa by uniquely derived structural attributes. The large degree of recent success achieved in this endeavor is manifested by the number of corroborated nested sets of structural features (see, for example, Figures 1, 14, and 19) which can serve as a basis for interpretations of evolutionary trends and processes.

An alternative approach, the analysis of the pattern of diversification in terms of general grades of evolutionary "advancement," tends to obscure phylogenetic (genealogical) patterns and conceals evolutionary sequences of structural change. We will precisely define the various actinopterygian groups, where possible, in terms of monophyletic lineages; in several cases insufficient information is available to define certain currently accepted major taxa as natural groups.

The relationships of the actinopterygian fishes to the other major groups of lower vertebrates will be examined briefly before we turn to a consideration of the relationships and general biology of the actinopterygian subgroups. An understanding of structural patterns and trends in the diversification of the ray-finned fishes is of critical importance for a meaningful analysis of actinopterygian functional morphology and evolution.

RELATIONSHIPS OF THE ACTINOPTERYGII

In recent years the interrelationships of the major groups of lower vertebrates have been considered in detail by various investigators, but a consensus has not emerged. Romer (1966), G. Nelson (1969a), Gardiner (1973), and Miles (1977) have all proposed differing hypotheses of how the Actinopterygii (ray-finned fishes), Actinistia (coelacanths), Dipnoi (lungfishes), and "rhipidistian" fishes and tetrapods are related (also see Forey, 1980; Jarvik, 1980; Lovtrup, 1977; Rosen *et al.*, 1981; Wiley, 1979a).

In Figure 1 we present one hypothesis of the interrelationships of these groups

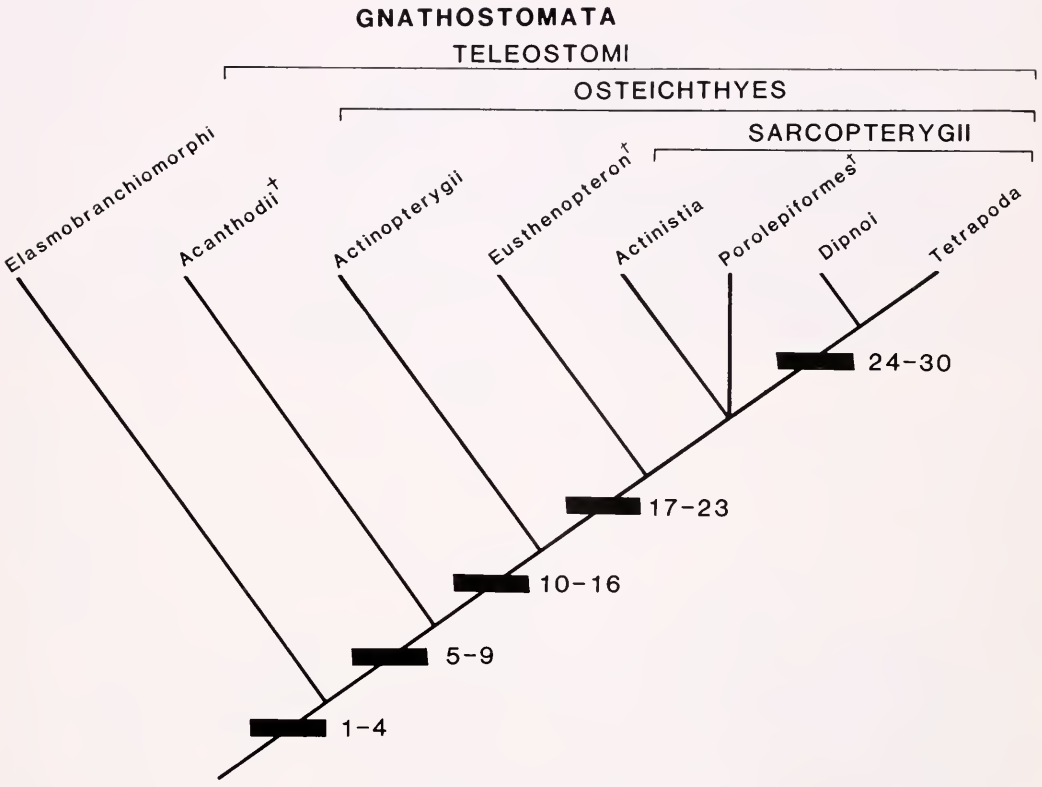


Figure 1. Branching diagram (cladogram) representing the phylogeny of the major groups of lower vertebrates. This and subsequent cladograms show the historical sequence of character acquisition in the lineage and reflects the genealogical relationships of the terminal taxa. The characters that indicate relationship between the various lineages are represented by a black bar at the appropriate level. Note that several of the characters listed on the cladograms apply only to living forms and thus do not corroborate the location of fossil taxa. The discovery of new fossil material or new anatomical features in extant taxa may change the level at which any given character indicates shared ancestry. The characters are: **1,** the presence of three semicircular canals (placoderms also share this feature); **2,** the presence of a ventral otic fissure between the embryonic trabecular and parachordal segments of the chondrocranium; **3,** the presence of a lateral occipital braincase fissure; **4,** five other characters listed by Rosen *et al.* (1981) including branchial arches consisting of basibranchial, hypobranchial, ceratobranchial, epibranchial and pharyngobranchial elements, and internal supporting girdles for the pectoral and pelvic appendages: for further discussion of elasmobranchiomorphs and other characters at this level see Maisey, 1980, 1982; Schaeffer, 1981; Schultze and Trueb, 1981; **5,** ossified dermal opercular plate(s) covering the gills laterally; **6,** presence of an interhyal bone in the hyoid arch (Gardiner, 1973: 129); **7,** branchiostegal rays present (Miles, 1973); **8,** mandibular depression primarily mediated by posteroventral rotation of the hyoid apparatus (inferred from the similarity of the hyoid—palatoquadrate relationships to that in osteichthyans (see Lauder, 1980c; Miles, 1973), and a mandibulohyoid ligament is inferred to have been present); **9,** sclerotic ring present (see Miles, 1973; Moy-Thomas and Miles, 1971); **10,** transversi ventrales gill arch muscles present (Wiley, 1979); **11,** interarcuales ventrales muscles present (Wiley, 1979); **12,** hypohyal bones present in the hyoid arch (Gardiner, 1973; Miles, 1973), **13,** medial insertion of the adductor mandibulae complex in the mandibular fossa (Lauder, 1980b); **14,** pleural ribs present (Schaeffer, 1968); **15,** lepidotrichia present (see text); **16,** unique ossification pattern in the dermal shoulder girdle (suprascapular, supracleithrum, cleithrum, and clavicle; Schaeffer, 1968)—many other characters corroborating a monophyletic osteichthyes are listed in Rosen *et al.* (1981); **17,** true enamel present on the tooth surface (Smith, 1978); **18,** double articulation of the hyomandibula with the neurocranium (Gardiner, 1973); **19,** unique supporting skeleton in paired fins; **20,** presence of an endoskeletal urohyal (Patterson, 1977); **21,** last gill arch articulates with base of preceding arch (Rosen *et al.*, 1981: 257); **22,** muscular lobes form the base of pelvic and pectoral appendages (Rosen *et al.*, 1981); **23,** anocleithrum subdermal (Rosen *et al.*, 1981; additional characters are also given in this paper); **24,** presence of a choana (see Rosen *et al.* [1981] for a detailed discussion of this controversial character); **25,** structure of the pelvic girdle (Rosen *et al.*, 1981); **26,** the presence of multiple pharyngoclaviculari muscles (Wiley, 1979a); **27,** numerous other features of soft anatomy such as partially divided conus arteriosus, an atrial septum, and ciliation of larval forms (see Gardiner, 1973; Rosen *et al.*, 1981; Whiting and Bone, 1980); **28,** dermal bone pattern covering the braincase; **29,** loss of interhyal; **30,** structure of the pelvic and pectoral appendage (see Rosen *et al.* [1981] for an extended discussion).

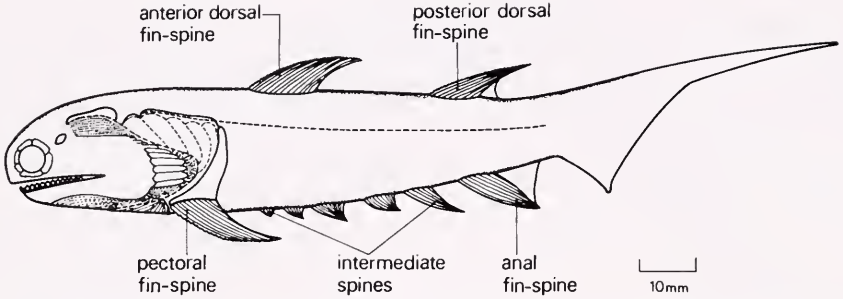


Figure 2. *Climatius reticulatus*, a Lower Devonian acanthodian fish. (From Moy-Thomas and Miles [1971], courtesy of W. B. Saunders Publishing Co.)

based on an analysis of the distribution of various characters (listed in the caption). This figure indicates that the actinopterygians share a common ancestor with a group consisting of the coelacanths (Actinistia), lungfishes, and tetrapods, and that these two groups together share a common ancestor with the acanthodian fishes.

The Acanthodii, often very inappropriately called "spiny sharks," first appear in the fossil record in the Lower Silurian. They are the most primitive members of the teleostome fishes (Fig. 1) and are characterized by pectoral fin spines, strong spines anterior to the dorsal and anal fins, and the presence of numerous small bony plates which form a protective cover over the branchial chamber (Fig. 2). Primitively the acanthodian fishes possess two dorsal fins which have internal unsegmented stiffening rays (Moy-Thomas and Miles, 1971). These fishes have rather large eyes relative to their head size and are generally assumed to have fed in the midwater or on the surface.

The Actinistia or coelacanths (Fig. 3) are first known from the Middle Devonian and are represented today by the single genus, *Latimeria*, discovered in 1938 off East London, South Africa. The coelacanths have two dorsal fins, two external nostrils, and an intracranial joint—a division between the anterior and posterior portions of the cranium allowing the anterior (ethmosphenoid) portion to be elevated during feeding (see Lauder, 1980a; Thomson, 1966, 1967). The caudal fin of coelacanths has a characteristic diphycercal or "tassel shape" (Fig. 3) with a central caudal lobe flanked dorsally and ventrally by two additional lobes. In Devonian coelacanths the brain appears to have nearly filled the cranial cavity (Stensio, 1963) while in the recent *Latimeria* the brain in the adult is significantly smaller than the cranial cavity, occupying only the otico-occipital division of the braincase and less than 1 percent of the total endocranial volume (Nieuwenhuys *et al.*, 1977). Throughout the long evolutionary history of the actinists their morphology has remained remarkably constant although there has been a general trend towards a reduction in neurocranial ossification (see Forey [1981] for a consideration of coelacanth phylogeny).

The Dipnoi or lungfishes (Fig. 4) originated in the Lower Devonian and have a long history culminating in three extant genera (Thomson, 1969). The earliest lungfishes differ greatly from the living forms. Primitively lungfishes possess two dorsal fins, a mosaic pattern of dermal skull elements which are difficult to homologize with skull bones in other osteichthyian groups, and thick cosmoid scales. The modern genera of lungfishes, *Neoceratodus* (Australian; one species), *Protopterus* (African; four species), and *Lepidosiren* (South American, one

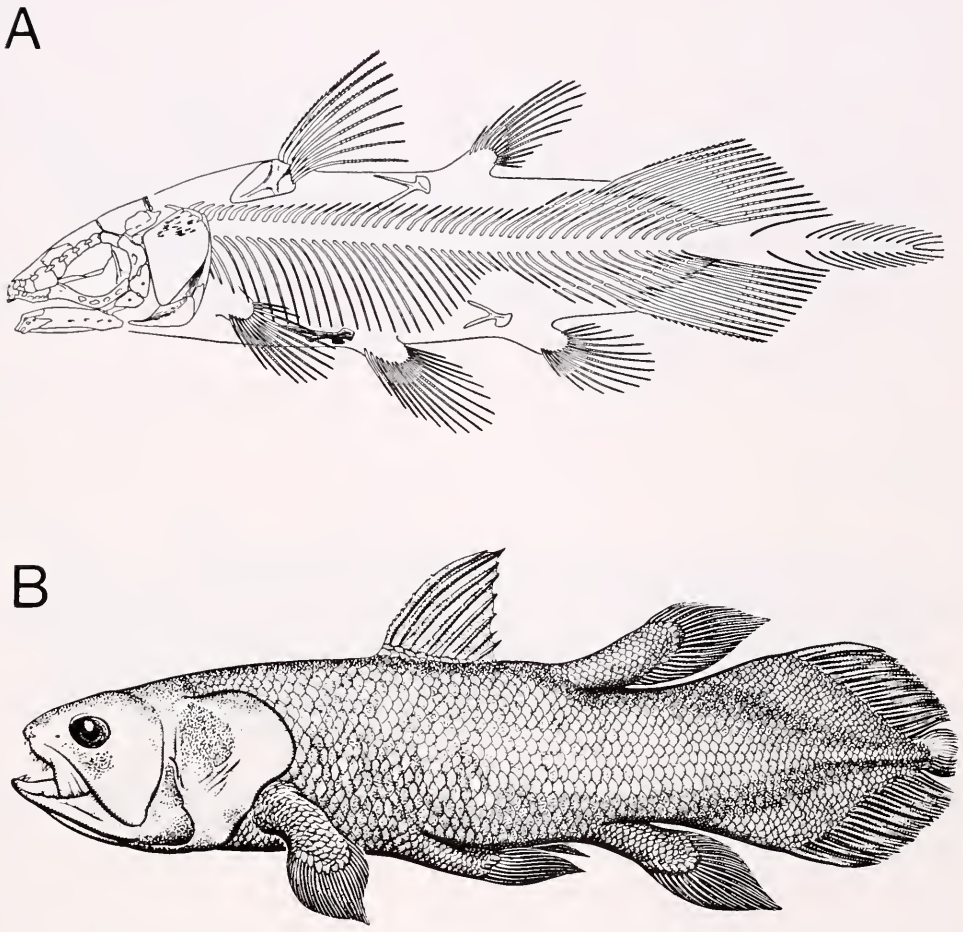


Figure 3. A. An early fossil coelacanth, *Diplurus newarki.* (From Schaeffer, 1952.) B. The living coelacanth, *Latimeria.* (From "The Vertebrate Body," 5th Ed. by A. S. Romer and T. S. Parsons. Copyright 1977 by W. B. Saunders Co. Reprinted by permission of Holt, Rinehart, and Winston Co.)

species) have scales embedded in the skin and have continuous dorsal, caudal, and anal fins (Fig. 4). Despite these specializations and reduced ossification in living forms, four primitive features have been retained in living lungfishes: three pairs of peculiar ridged tooth plates, the lack of marginal toothbearing jaw bones, an autostylic palatoquadrate fused to the neurocranium, and a greatly reduced hyomandibula. The Dipnoi share several important features of the circulatory system, as well as other characters (Fig. 1) with the Tetrapoda (Rosen *et al.*, 1981).

Rosen *et al.* (1981), in the course of examining the relationships of lungfishes, have also considered the phylogenetic position of the so-called rhipidistian fishes (Fig. 5). Although the rhipidistians have traditionally been considered as ancestral to tetrapods (Andrews and Westoll, 1970a, b; Romer, 1966; Thomson, 1964), Rosen *et al.* (1981) show that one group of "rhipidistians," the Porolepiformes, is related to coelacanths and choanates (Fig. 1), while *Eusthenopteron* is considerably more primitive than had previously been supposed (Fig. 1). The

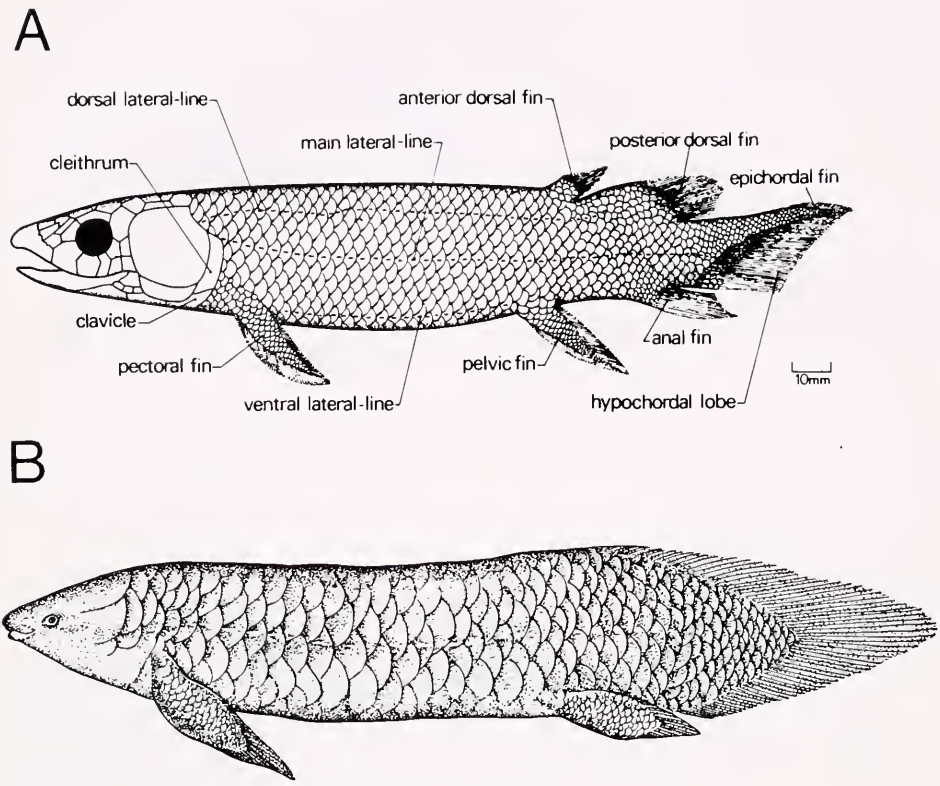


Figure 4. A. A Middle Devonian lungfish, *Dipterus valenciennesi*. (From Moy-Thomas and Miles [1971], courtesy of W. B. Saunders Publishing Co.) B. The living Australian lungfish, *Neoceratodus forsteri*. (From Romer and Parsons [1977], courtesy of C.B.S. College Publishing.)

Rhipidistia are thus a paraphyletic group and are not characterized by uniquely derived features. Porolepiformes possess two dorsal fins, and many "rhipidistians" also have an intracranial kinetic joint. The ventral part of this joint appears to be a primitive teleostome feature (Fig. 1) while the dorsal portion of the joint appears to be nonhomologous in coelacanths and "rhipidistians" (Rosen *et al.*, 1981; Wiley, 1979b, 1980). The functional anatomy of the kinetic mechanism is also very different in these two groups (Thomson, 1967).

Turning now to the Actinopterygii or ray-finned fishes, named for the dermal, segmented, ray-like supports within the fins, it is clear that despite considerable research on other osteichthyian groups, few if any investigators have explicitly tested the hypothesis of actinopterygian monophyly. The Actinopterygii have undergone an extensive radiation since their first well-established appearance in the Lower Devonian, and this tremendous diversity of morphology and habit as well as the historical interplay between neontology and paleontology (Patterson, 1982) has hindered the development of a comprehensive definition of the Actinopterygii. Actinopterygian monophyly is usually assumed.

Patterson (1982) has recently investigated the question of actinopterygian monophyly in detail and has concluded that the principal difficulty in characterizing the Actinopterygii has been the confusing pattern of character distribu-

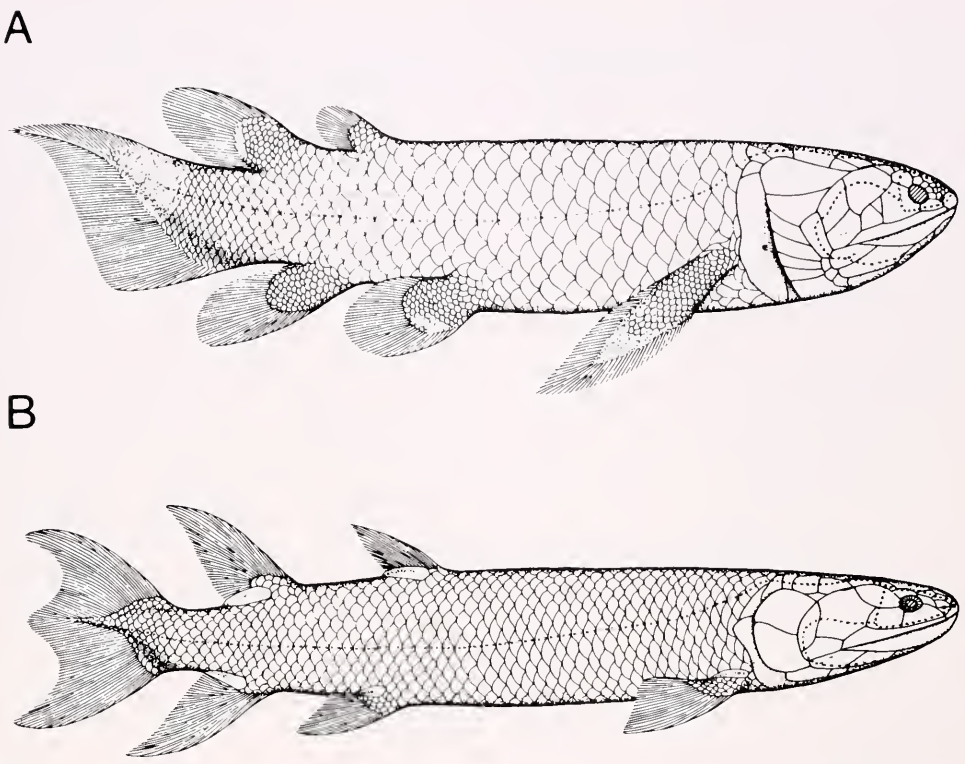


Figure 5. A. *Holoptychus,* a Late Paleozoic porolepiform. Rosen *et al.* (1981) place the porolepiformes at the node joining the actinists and the Choanata (Fig. 1) thus forming an unresolved trichotomy. Porolepiform anatomy is poorly known. B. *Eusthenopteron foordi,* an Upper Devonian sarcopterygian placed by Rosen *et al.* (1981) as the sister group to the sarcopterygians. Many of the characters shared by *Eusthenopteron* and early tetrapods and commonly believed to be indicative of relationship now appear also to be shared with coelacanths, porolepiforms, and lungfishes. These features thus corroborate a monophyletic assemblage composed of *Eusthenopteron* and the Sarcopterygii (Fig. 1). (From Andrews [1973], reprinted by permission of the Council of the Linnean Society of London.)

tion when living relic forms such as *Polypterus* and *Lepisosteus* are considered. Patterson (1982: Fig. 3B) lists seven characters of the Actinopterygii which unite the primitive fossil form *Cheirolepis*, *Polypterus*, and all higher ray-finned fishes into a monophyletic group (Fig. 6). Two of these are discussed here.

Actinopterygian fishes share a unique scale histology, the ganoid scale, with an outer lamellar layer (ganoine), a central dentinous layer with vascular canals, and a deep layer of spongy bone (Goodrich, 1908; Gross, 1966; Moy-Thomas and Miles, 1971; Patterson, 1982; Pearson, 1982; also Schultze, 1977). These scales are rhomboid in shape, have a dorsally directed peg that fits into a socket on the adjacent dorsal scale (Fig. 7D), and are arranged in sloping diagonal rows along the body (Fig. 7). A unique pectoral fin structure is shared by all actinopterygians which have an expanded propterygial element of the pectoral fin base and an extensive articular surface with the endoskeletal shoulder girdle (Jessen, 1972; Rosen *et al.*, 1981).

Rosen *et al.* (1981) mention two additional characters relevant to actinopterygian monophyly. 1) Acrodin, a dentinous tissue (Orvig, 1978), forms a cap on the teeth of many ray-finned fishes (Patterson, 1982), including many primitive fossil taxa and *Polypterus*. 2) The pelvic gir-

dle of actinopterygians has a greatly expanded metapterygium which supports the fin radials. The metapterygium may be composed of smaller separate cartilages in juveniles, but in adults the cartilages are generally fused together. The ontogenetic fusion of internal pelvic cartilages into a larger adult structure is unique to ray-finned fishes. Early ray-finned fishes also possess a single dorsal fin (Figs. 6, 7). Acanthodians, actinistians, and lungfishes all primitively possess two dorsal fins while primitive actinopterygians, the paleoniscoid fishes, have only a single dorsal fin. This feature is remarkably constant throughout the entire actinopterygian radiation although the dorsal fin has been lost or highly modified in several groups, and in the more advanced teleostean fishes the fin is subdivided into an anterior spiny portion and a posterior soft-rayed section.

One last noteworthy feature of actinopterygians is the nature of the fin articulation: median fins are supported internally by paired segmented dermal rays (lepidotrichia), and these are attached to an internal skeleton which does not extend into the fin at the fin base. Between the distal ends of each pair of lepidotrichia lies an unsegmented actinotrich made of elastoidin, a fibrous collagenous protein (Arita, 1971; Geraudie and Meunier, 1980; Videler, 1975). This morphology may be correlated with an increase in fin mobility and greater maneuverability during locomotion. Actinotrichia are also found in coelacanths (Geraudie and Meunier, 1980) and bear a close similarity both in chemical composition and fine structure to selachian ceratotrichia. This raises the possibility that actinopterygian actinotrichia are homologous to selachian ceratotrichia (suggested by Goodrich, 1904), as both are composed of elastoidin, are not mineralized, and both consist of "giant collagenous fibers constructed of closely packed or fused fibrils aligned so that the banding (60–65 nm) of the collagen fibrils is in register throughout the fiber" (Geraudie and Meunier, 1980: 637; also see Patterson, 1977a: 113). Based on these data and the work of Goodrich (1904), Geraudie (1980), Kemp (1977), and Patterson (1977a), the following phylogenetic hypothesis of intrinsic fin supports may be proposed for future detailed examination. Collagenous fin rays composed of elastoiden are primitive for gnathostomes, with a derived state consisting of a terminal "actinotrich" located at the distal end of the fin rays, and lepidotrichia which are both segmented and ossified, corroborating a monophyletic Osteichthyes (Fig. 1). An ontogenetic study of dipnoan fin rays is needed to flesh out this hypothesis, as Patterson (1977a) suggests that the dipnoan "camptotrichia" are really ceratotrichia/actinotrichia with an outer ossified face, a view not considered by Geraudie and Meunier (1982) in their analysis of camptotrich structure.

PRIMITIVE ACTINOPTERYGIAN FISHES

The early actinopterygian fishes are usually included in the Infraclass Chondrostei (Alexander, 1967; Bailey and Cavender, 1971; Gosline, 1971; Lagler *et al.*, 1977; J. Nelson, 1976; Romer, 1966). This grouping results more from a lack of information on the relationships of the early ray-finned fishes than from the expectation that "chondrosteans" actually form a natural group. The "Chondrostei" usually includes a diverse assemblage of fossil and living taxa and is demonstrably paraphyletic (Schaeffer, 1973). Since this grouping tends to obscure the phyletic relationships of primitive actinopterygians, we will follow Patterson (1982) in restricting use of Chondrostei to refer to a monophyletic clade composed of sturgeons, paddlefishes, and closely related fossil groups (Fig. 6; see below for further discussion).

The interrelationships of the primitive living actinopterygians have been relatively well established (Fig. 6) largely as

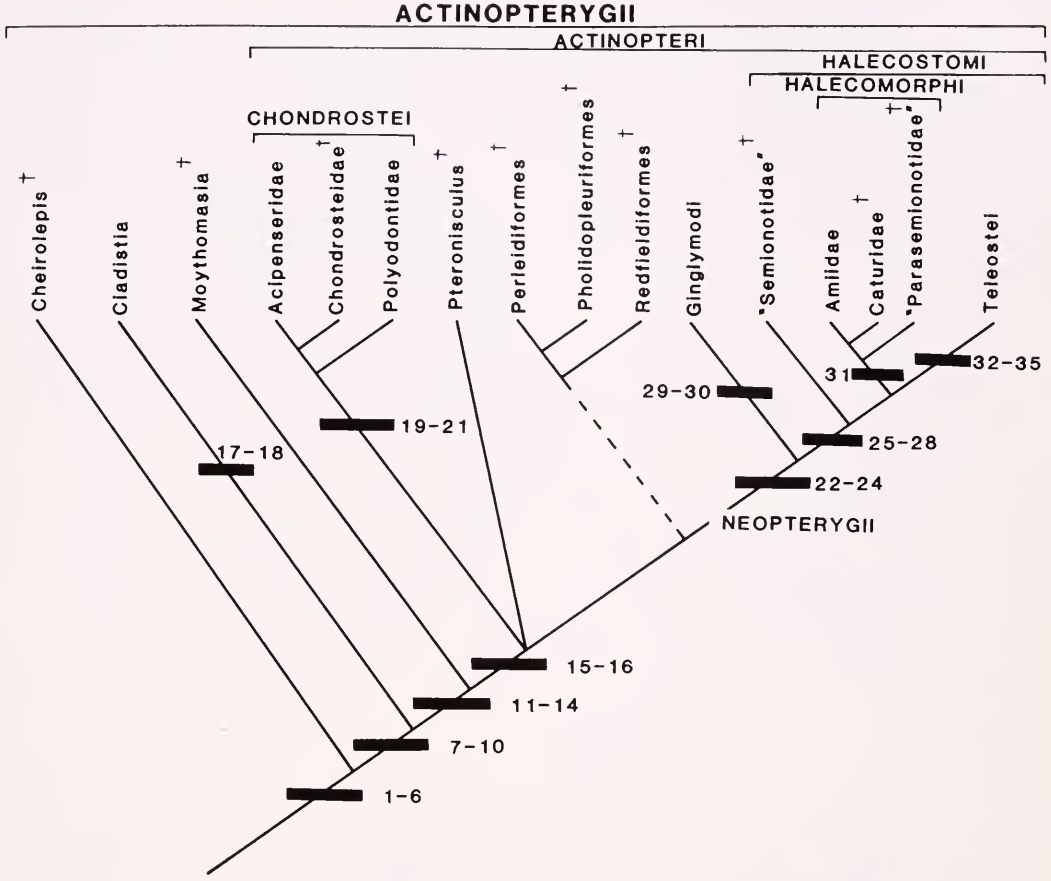


Figure 6. Branching diagram (cladogram) showing one hypothesis of the relationships between the main actinopterygian subgroups. Taxa with no living representatives are indicated with a dagger. Patterson (1982) provides an extensive discussion of the relationships of primitive actinopterygians and many of the characters listed here are abstracted from his paper. The characters are: **1,** presence of a single dorsal fin; **2,** a pectoral propterygium (see Rosen *et al.,* 1981); **3,** ganoin, **4,** anterodorsal peglike process on the scales; **5,** jugal pitlines; **6,** mandibular sensory canal enclosed in the dentary bone; **7,** autosphenotic and large opisthotic bone in the braincase; **8,** acrodin caps on teeth; **9,** pelvic plate present (see Rosen *et al.,* 1981); **10,** numerous features of soft anatomy including brain development, jaw muscles, and gill arch muscles (Wiley, 1979; Nieuwenhuys, 1982; Patterson, 1982; Lauder, 1980b); **11,** a perforated propterygium; **12,** basal fulcra on dorsal caudal margin; **13,** supra-angular bone present in lower jaw; **14,** hemopoietic organ above the medulla oblongata; **15,** fringing fulcra on fins; **16,** spiracular canal; **17,** dorsal finspines; **18,** ontogenetic fusion of infraorbitals with the maxilla (see Patterson [1982] and Daget [1950] for additional characters); **19,** absence of myodomes (Schaeffer, 1973); **20,** fusion of premaxillae, maxillae, and dermopalatines (Schaeffer, 1973); **21,** anterior palatoquadrate symphysis (Jollie, 1980); **22,** fin rays equal in number to their supports in the dorsal and anal fins (Patterson and Rosen, 1977); **23,** upper pharyngeal dentition consolidated (Patterson and Rosen, 1977); **24,** clavicle lost or reduced to small plate lateral to cleithrum (see Patterson and Rosen (1977) who also provide several other characters); **25,** mobile maxillary bone in the cheek; **26,** interopercular bone present; **27,** median neural spines; **28,** quadratojugal lost or fused with quadrate (Patterson and Rosen, 1977); **29,** opisthocoelous centra; **30,** a series of toothed infraorbital bones (see Wiley (1976) for many other characters); **31,** both the symplectic bone and the quadrate contribute to the jaw articulation (see Patterson [1973] for further discussion of this clade); **32,** the presence of uroneurals (elongated ural neural arches); **33,** unpaired basibranchial toothplates; **34,** a mobile premaxilla; **35,** internal carotid foramen enclosed in the parasphenoid (Patterson, 1977a). Patterson (1977) also mentions two other features as tentative teleostean features: seven epurals, and a pectoral propterygium fused with the first pectoral fin ray. Living teleosts share many features in the jaw musculature (see text; Lauder 1980c), including loss of the anterior (suborbital) jaw adductor component.

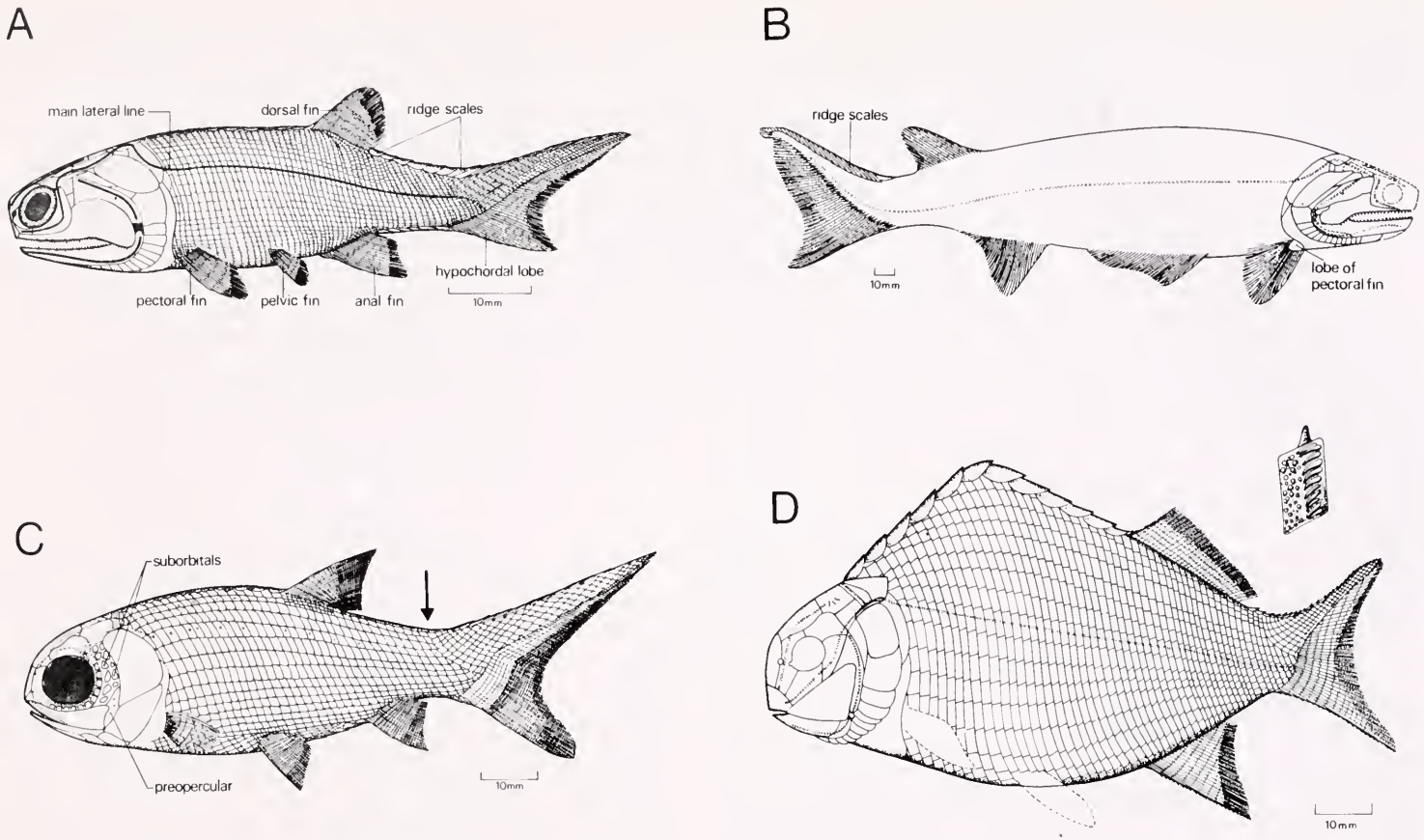


Figure 7. Gross morphology of some representatives of early actinopterygian fishes. A. *Moythomasia nitida* (Upper Devonian) (Fig. 6). B. *Cheirolepis canadensis* (Middle-Upper Devonian) (Fig. 6). C. *Aduella blainvillei* (Lower Permian), arrow points to the "chondrostean hinge." D. *Androichthys tuberculatus* (Lower Carboniferous), a member of the deep-bodied family Chirodontidae. Note the long closely fitting scale rows and the enlarged scale (D, upper right) showing the dorsal peg which inserts into a ventral socket on the scale above. (From Moy-Thomas and Miles [1971], courtesy of C.B.S. College Publishing.)

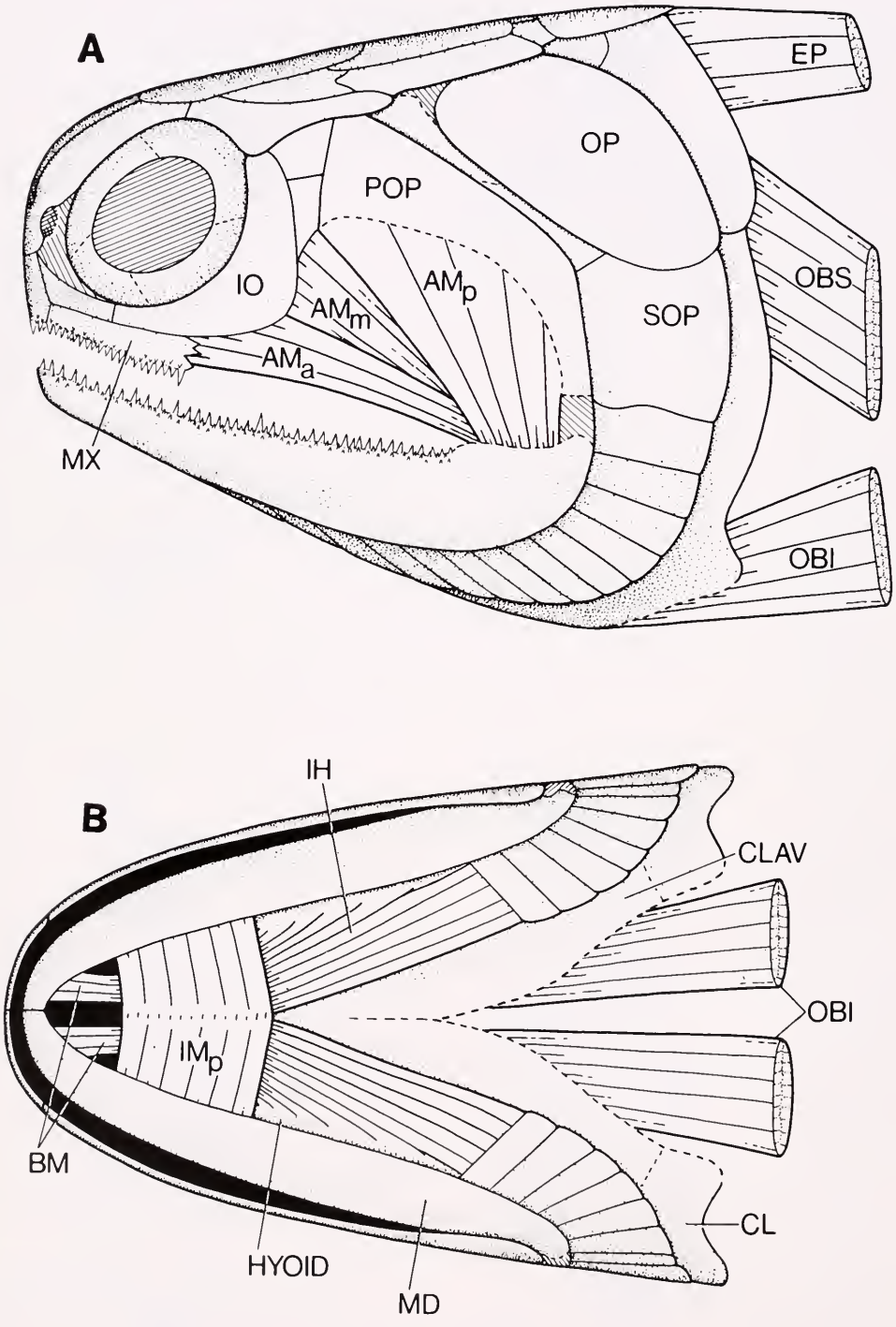
the result of the recent work of Jollie (1980), Patterson (1973, 1975, 1982), Rosen *et al.* (1981), and Wiley (1976). The interrelationships of the primitive fossil taxa remain problematical. Only three fossil genera have been assigned a position in actinopterygian phylogeny that is corroborated by uniquely derived characters: *Cheirolepis* (Fig. 7B), *Moythomasia* (Fig. 7A) and *Pteronisculus* (see Fig. 6; Patterson, 1982). Schaeffer (1973) has also identified several possible monophyletic assemblages among lower actinopterygians. The Devonian *Cheirolepis* (Pearson and Westoll, 1979) is the most primitive known ray-finned fish (Fig. 6).

The structure of the skull in these early actinopterygians (Fig. 8) reflects their generally predaceous habit (Pearson and Westoll, 1979). Simple conical teeth are present along the marginal jaw bones and on many of the dermal bones lining the buccal cavity. The dermal cheek bones form a relatively solid plate with the large maxilla occupying much of the cheek and attaching posteriorly to the preoperculum. Lateral movements of the cheek and palatoquadrate were relatively limited (Lauder, 1982a). An operculum and subopercular covered the gills laterally and a series of smaller bony plates, the branchiostegal rays, extended posterolaterally from the hyoid apparatus (Fig. 8). The eye and nasal openings were located far anteriorly. Paleonisciform fishes possessed a tripartite adductor mandibulae (Fig. 8: AMa,m,p) with a posteroventral fiber orientation. The primitive gnathostome condition is retained in the ventral head musculature (Fig. 8; Lauder, 1980b) with an intermandibularis posterior extending between the mandibular rami and an interhyoideus connecting the branchiostegal rays and hyoid to the fascia dorsal to the intermandibularis posterior. Incidentally, this general arrangement of the buccal floor musculature appears to have been a very conservative feature in lower vertebrate evolution, as a very similar condition is found in coelacanths, lungfishes, and salamanders.

The braincase of these early ray-finned fishes exhibits several remarkable features (Fig. 9). A ventral otic fissure (Fig. 9: vof), cartilage filled in life, represents a persistent division between the embryonic parachordal and trabecular elements of the chondrocranium and lies just posterior to the hypophysis. An additional fissure, the lateral occipital fissure of the braincase (Fig. 9: lof) provides an exit for the vagus nerve, represents a persisting embryonic metotic fissure, and may not have been filled with cartilage in adult paleoniscoids (Gardiner and Bartram, 1977; Patterson, 1975; Schaeffer and Dalquest, 1978). It is important to note that the adult braincase of many primitive actinopterygians was fully ossified and completely sutureless, a condition that prohibited further growth (Patterson, 1975).

In contrast to the teleost and haleomorph actinopterygians (see below) in which a suction feeding mechanism is developed (a negative pressure is created in the buccal cavity and used to draw in prey with the inflow of water as the mouth is opened), most paleoniscoid fishes had only a limited ability to expand the buccal cavity (Schaeffer and Rosen, 1961; Lauder, 1982a) and thus must have primarily used their body velocity to overtake and capture prey rather than the "ambush predator" strategy used so successfully by many teleosts. Mouth opening in all non-haleocostome actinopterygians is accomplished by contraction of the hypaxial and sternohyoideus muscles (Lauder, 1980c; 1982a). These muscles mediate posteroventral hyoid movement which causes mandibular depression. Elevation of the neurocranium during prey capture also contributes significantly to the increase in gape.

The primary use of body velocity in prey capture is reflected in the structure of the locomotory apparatus in the early ray-finned fishes and suggests several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functional correlates of body form. The early actinopterygians are unique among lower vertebrates in possessing a single dorsal fin, and generally lateral body and fin profiles are not concentrated far posterior to the center of gravity. Webb (1976, 1977, 1978) has examined fast-start performance in teleost fishes and has concluded that the ability to rapidly accelerate from a rest position (of great importance to ambush predators) is largely a function of lateral body and fin area and the mass of body musculature, higher values of both giving improved fast-start performance. The paleoniscoid fishes would have had a rather poor fast-start performance since fin area is relatively small, caudal fin shape is not designed to rapidly generate anteriorly directed forces (Thomson, 1976; Webb, 1982) and neural and haemal spines were not firmly attached to vertebral centra (Lauder, 1980d; Schaeffer, 1967).

The caudal fin in early actinopterygians is heterocercal in shape, the notochord and vertebral elements extending into the upper (epichordal) lobe while the hypochordal lobe (Fig. 7A) possesses little to stiffen it except the dermal fin rays. This external and internal morphological asymmetry in tail structure may have resulted in an "asymmetrical" thrust (Thomson, 1976) directed anteroventrally. One of the fundamental functional changes in actinopterygian evolution is often held to be the modification of tail structure to generate an anteriorly directed symmetrical thrust, the correlated reduction in scale weight (and thus specific gravity), and evolution of a gas-filled swimbladder from the primitive lunglike pharyngeal diverticulum. The role of the swimbladder in allowing the achievement of neutral buoyancy was of potential importance both for a reduction in energy expenditure needed to maintain a constant level in the water column (Alexander, 1966a) and in the removal of functional constraints on caudal and pectoral fin structure. Many primitive actinopterygian fishes, however, possessed a very high aspect ratio tail with complete external symmetry (e.g., *Bobasatrania*, *Platysomus*, *Chirodus*, and *Dorypterus*; see Schaeffer, 1973: 217). These forms also had enlarged stiffening rays in the hypochordal fin lobe. In the absence of experimental data on the function of primitive actinopterygian caudal fins, it is perhaps unwise to speculate about the direction of thrust produced and to generalize too broadly about the "inefficiency" of asymmetrical caudal structure.

Two other groups of fossil ray-finned fishes deserve mention. A deep-bodied radiation of primitive forms is represented by the platysomoids, of which *Adroichthys* (Fig. 7D) is a member. A second lineage is composed of the redfieldiiform and perleid fishes (Fig. 6), although monophyly of this assemblage has not been conclusively established (see Schaeffer, 1973; Hutchinson, 1973; Brough, 1939). These fishes share several general features with the neopterygian fishes, including a nearly vertically oriented palatoquadrate allowing greater expansion of the orobranchial chamber, a

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Figure 8. General structure of the skull in a palaeoniscoid fish (*Moythomasia nitida*). The cheek is covered with a solid plate of dermal bone composed of infraorbital bones, a preoperculum, and a large expanded maxillary bone, partially removed to show the underlying adductor musculature. The oblique orientation of the preoperculum indicates the posterior inclination of the palatoquadrate. The dentary lacks a coronoid process. Mouth opening during feeding occurred by lifting of the upper jaw and by depression of the mandible via posterior movements of the hyoid apparatus. Primitive actinopterygians possessed three divisions of the adductor mandibulae, anterior (AMa), medial (AMm), and posterior (AMp). (From Lauder [1982a], courtesy of the American Society of Zoologists.)

Other Abbreviations: BM, branchiomandibularis; CL, cleithrum; CLAV, clavicle; EP, epaxial muscles; IH, interhyoideus muscle; IMp, intermandibularis posterior muscle; IO, infraorbital bones; MX, maxilla; OBS, obliquus superioris muscle; OBI, obliquus inferioris muscle; OP, operculum; POP, preoperculum; SOP, suboperculum.

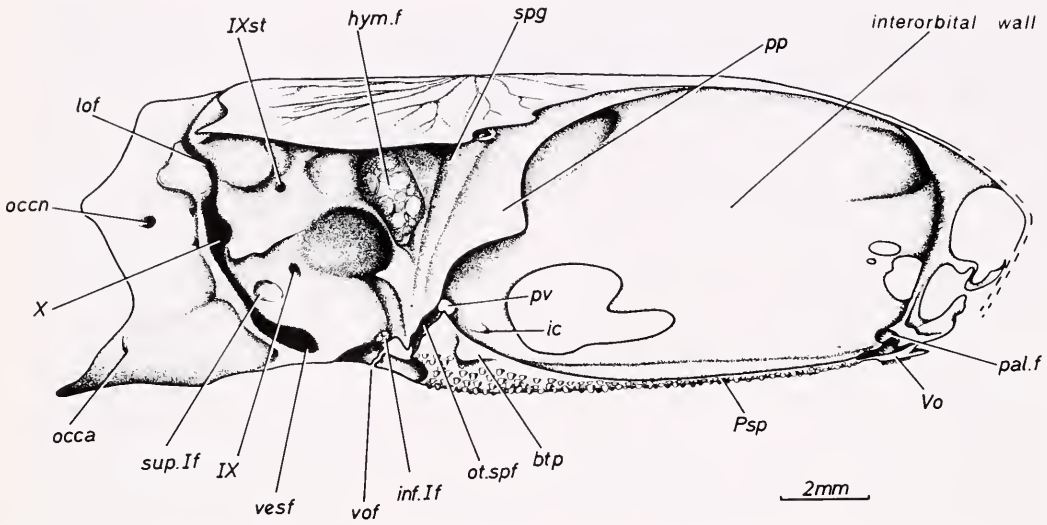


Figure 9. The braincase of a paleoniscoid fish (lateral view of the right side) showing the interorbital wall, the ventral otic fissure (vof), the lateral occipital fissure (lof) and exits for the vagus nerve (X), glossopharyngeal nerve (IX), supratemporal branch of IX (IXst), the parasphenoid bone (Psp), vomer (Vo), foramen for the pituitary vein (pv) and for the internal carotid artery (ic). (After Gardiner [1973], reprinted by permission of the Council of the Linnean Society of London.)

Other Abbreviations: btp, basipterygoid process; hym.f, hyomandibular facet; inf.If, articular facet for infrapharyngobranchial I; occa, occn, foramina for the occipital artery and nerve; ot.spf, oticosphenoid fissure; pal.f, articular facet for palatine bone; pp, postorbital process; spg, spiracular groove; sup.If, articular facet for suprapharyngobranchial I; vesf, vestibular fontanelle.

coronoid process on the mandible, and the expansion of one of the upper branchiostegal rays.

The early actinopterygian fishes represent a relatively limited radiation which remained morphologically rather uniform in basic plan. The first major changes in feeding and locomotory patterns occur in the neopterygian fishes, but first we must examine the living survivors of the early ray-finned fishes, the bichir and reedfish *Polypterus* and *Erpetoichthys* (Cladistia), and the sturgeons and paddlefishes (Chondrostei). Rosen *et al.* (1981) proposed using Cope's (1871) term Actinopteri to refer to all actinopterygians more derived than cladistians (see Fig. 6), and this usage is followed here (also see Patterson, 1982).

The Cladistia contains the single family Polypteridae with two genera, *Polypterus* and *Erpetoichthys* (=*Calamoichthys*; see Swinney and Heppell, 1982), and has been the subject of extensive debate in the literature of the last hundred years. Probably no other group of living fishes has been placed, at one time or another, in so many widely differing major taxonomic groups. An early view (Huxley, 1861; Cope, 1871; see Patterson, 1982, for a historical review) was that the polypterids were members of the Sarcopterygii or "lobe-finned fishes" (Fig. 1), an hypothesis based primarily on the structure of the pectoral fin in *Polypterus* (Fig. 10), which consists of a proximal lobelike extension from the body and a fan-shaped distal array of fin rays (Fig. 10A). Jarvik (1980) still supports this view.

This suggestion has been largely supplanted in recent years by the hypothesis that polypterids are sufficiently distinct to warrant recognition as a separate subclass of the Osteichthyes, the Brachio-

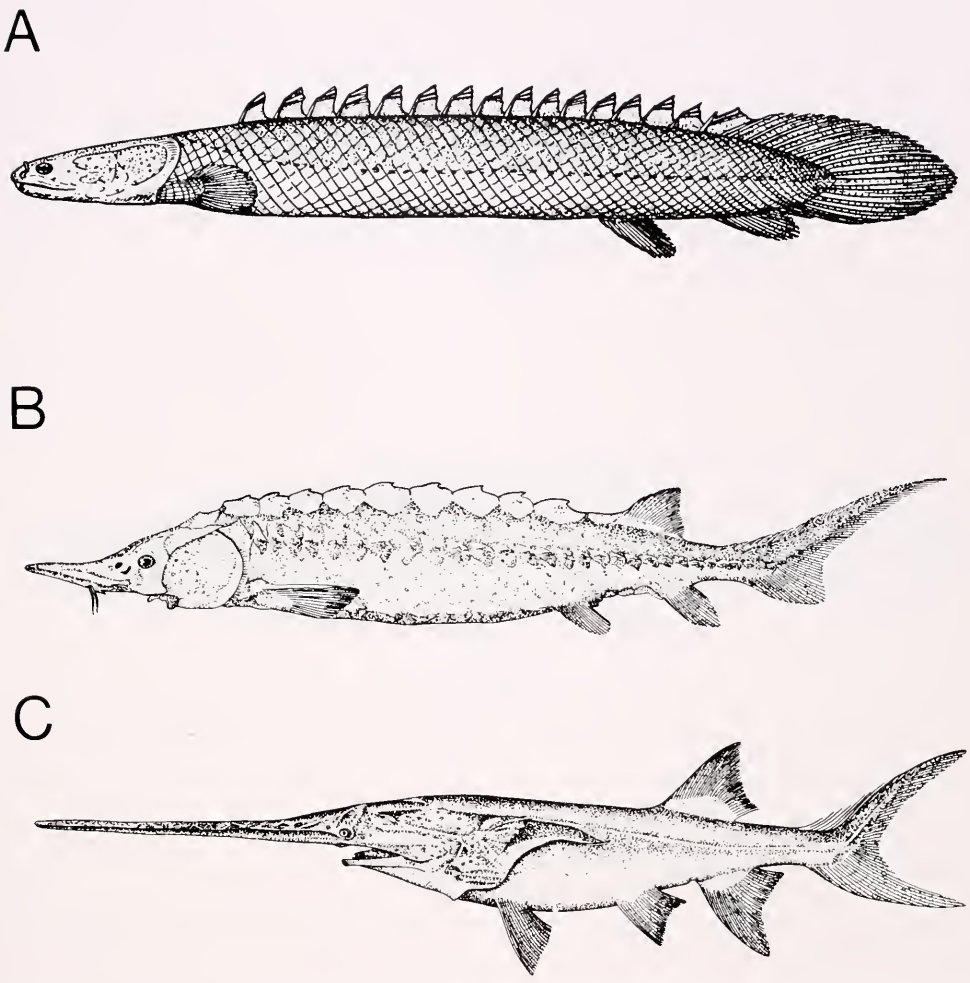


Figure 10. A. A representative of the genus *Polypterus*. B. *Scaphirhynchus*, a sturgeon from the Mississippi drainage. C. *Polyodon spathula*, also from the Mississippi. (From "The Vertebrate Body," 5th Ed. by A. S. Romer and T. S. Parsons. Copyright 1977 by W. B. Saunders Co. Reprinted by permission of Holt, Rinehart, and Winston.)

pterygii (e.g., McAllister, 1968; G. Nelson, 1969a). More recently, however, Gardiner (1973), Schaeffer (1973), Wiley (1979a), and especially Patterson (1982) have provided convincing evidence, summarized in Figure 6, that the polypterids represent highly specialized survivors of primitive actinopterygian fishes. Romer (1966), Gardiner (1967), and Andrews *et al.* (1967) have also held this view. Nieuwenhuys (1967, 1982) has allied *Polypterus* with the Actinopterygii on neuroanatomical evidence, as has Lovtrup (1977) on otolith structure and lens proteins.

The Cladistia are hypothesized to be monophyletic based on the dorsal finspine pattern (Fig. 10A), the presence of a series of spiracular ossicles, and the structure of the urohyal and parasphenoid, among many other uniquely derived features (Daget, 1950; see Patter-

son, 1982). The genus *Polypterus* (bichirs) is composed of 10 species, all very similar in appearance. A row of dorsal finlets extends down the back (Fig. 10), each finlet having an anterior spine supporting a thin membraneous web posteriorly. These finlets are elevated during active swimming but lie flat when the fish is inactive. A primitive actinopterygian feature retained by *Polypterus* is the thick covering of rhomboid scales arranged in oblique rows along the body (Pearson, 1981). The internal skeleton is well ossified, the tail is modified into a so-called diphycercal or symmetrical shape, and a spiracle connects the buccal cavity with the surrounding water via a short spiracular canal opening onto the dorsal head surface. The cranial anatomy of *Polypterus bichir* has been described in detail by Allis (1922). Young *Polypterus* possess a pair of relatively large external gills which extend posteriorly from the hyoid arch. Adult *Polypterus* are able to breathe air and have a pair of highly vascularized lungs which arise ventrally from a diverticulum in the floor of the pharynx. The lungs are asymmetrical in size, the right extending much further posteriorly than the left. In view of the widespread occurrence of ventral lunglike diverticula in primitive osteichthyian groups, the presence of lungs and probably the occurrence of external gills in young may be a primitive feature of actinopterygian fishes that has been retained in *Polypterus*. Although most commonly seen at a size of about 15 to 20 cm, some species of *Polypterus* can grow to well over a meter in total length.

The other genus included in the Polypteriformes is *Erpetoichthys* with one species, *E. calabaricus* (the reedfish). This fish is elongate in form and considerably thinner than *Polypterus* with a round ropelike body. *Erpetoichthys* lacks pelvic fins but is similar to *Polypterus* in all major characters outlined above. The Polypteridae are only found in the freshwaters of tropical Africa and are generally distributed along lake shores.

The two remaining groups representing living survivors of early ray-finned fishes are the sturgeons, family Acipenseridae, and the paddlefishes, family Polyodontidae. These two families and the allied fossil forms such as *Chondrosteus* are united into the Chondrostei (Fig. 6). Schaeffer (1973), Jollie (1980), and Patterson (1982) have examined the evidence supporting the Chondrostei as a monophyletic lineage (see Fig. 6; characters 19–21). Several of the characters shared by the two living families are reductive ones (such as absence of myodomes) and may have evolved independently, but current evidence does seem to corroborate a monophyletic Chondrostei.

The family Acipenseridae, first known from Upper Cretaceous fossils, contains four genera arranged in two subfamilies. The subfamily Acipenserinae, containing *Acipenser* (about 20 species) and *Huso* (2 species), is found in Eurasia and North America; some species live only in freshwater (where all species spawn) while others have part of the lifecycle in the ocean. The subfamily Scaphirhynchinae includes the genus *Pseudoscaphirhynchus* (3 species), which is confined to Asia, and *Scaphirhynchus* (2 species) (See Fig. 10B). The different genera and species are distinguished on the basis of mouth shape and scalation, while the subfamilies differ in the occurrence of a spiracle: present in the Acipenserinae and absent in the Scaphirhynchinae. The body shape of sturgeons (Fig. 10B), the presence of a heterocercal tail, and a mainly cartilaginous skeleton suggested to several investigators early in this century that sturgeons should be included in the Selachii. These features are actually either reductions from a primitive actinopterygian condition (an ossified skeleton) or merely represent the retention of primitive characters (the heterocercal tail). Sturgeons

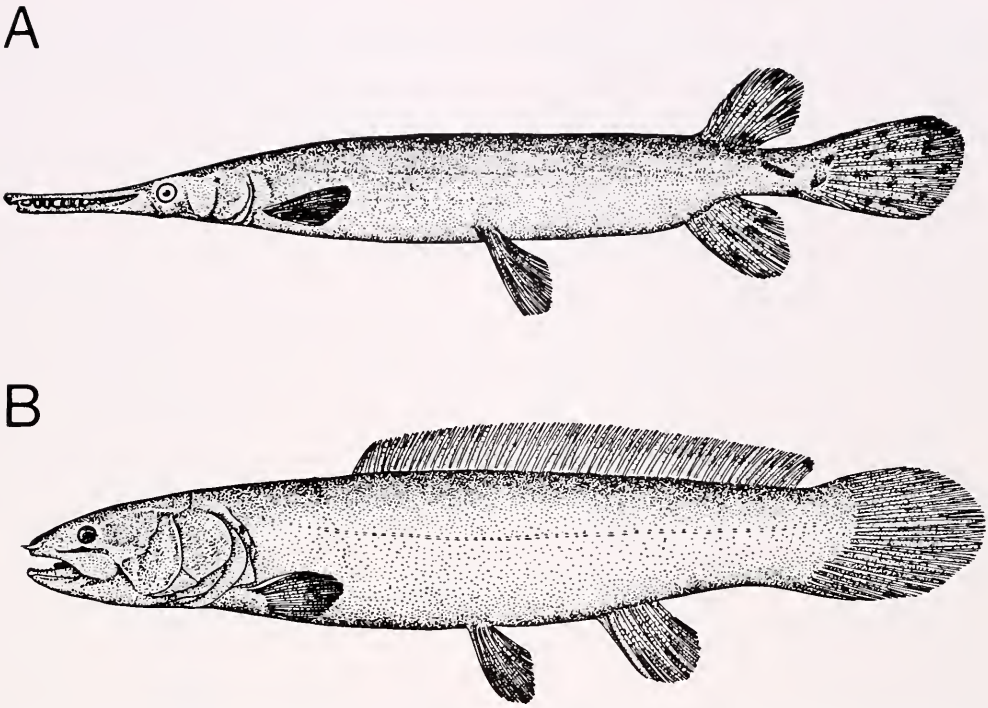


Figure 11. A. *Lepisosteus*, a living representative of the Ginglymodi. B. *Amia calva*, a living halecomorph fish. (From "The Vertebrate Body," 5th Ed. by A. S. Romer and T. S. Parsons. Copyright by W. B. Saunders Co. Reprinted by permission of Holt, Rinehart, and Winston.)

are peculiar in having scales modified into five rows of bony scutes which run the length of the body (Fig. 10B), greatly reduced teeth and jaws, and a large extended fleshy rostrum with barbels used in rooting for food on the bottom. Sturgeons, especially European species, may grow to an enormous size, record individuals weighing in at over 3,000 lbs.

The family Polyodontidae consists of two living genera, each with one species, with a disjunct distribution. *Polyodon spathula* (Fig. 10C) occurs in the Mississippi drainage of the United States. It has a very elongate snout with minute barbels, and long gill rakers for straining plankton from the water (Rosen and Hales, 1981). *Psephurus gladius* differs considerably in morphology from the American paddlefish and is found in the Yangtze River basin of China. The mouth can be protruded to feed on small benthic organisms, and the snout is considerably shorter than in *Polyodon*. Both genera have greatly reduced scalation. Paddlefishes usually reach a maximum size of about 2 meters. The first fossil record of the Family Polyodontidae occurs in the Upper Cretaceous with the genus *Paleopsephurus wilsoni* from Montana.

THE GINGLYMODI AND HALECOMORPHI

The Neopterygii (Fig. 6) contains two major groups, the Ginglymodi containing only the family Lepisosteidae (gars), and the Halecostomi (Fig. 11). The Halecostomi also consists of two major groups one of which, the Halecomorphi, containing

several fossil taxa and the living genus *Amia*, will be considered here while the other, the Teleostei, will be examined extensively below. Patterson and Rosen (1977) have recently given both the Teleostei and Halecomorphi the rank of Subdivision in the Division Neopterygii.

Some of the characters which have been used to define the neopterygian fishes (Fig. 6: characters 22–24) are the presence of an equal number of fin rays and fin ray supports in the dorsal and anal fins (primitively the number of fin rays exceeds the number of supports) and the occurrence of a symplectic bone which develops as a separate ossification center in the hyomandibular cartilage. Patterson (1973), Patterson and Rosen (1977), Wiley (1976), and Bartram (1977) provide extensive evidence for monophyly of the Neopterygii.

The Ginglymodi have been recently reviewed by Wiley (1976), who has provided a long list of characters shared by members of this group, including very elongate jaws with toothed infraorbital bones on the upper jaw (Fig. 12A), opisthocoelous vertebral centra, and teeth containing plicidentine. Gars have elongate bodies with the dorsal fin located far posteriorly on the body (Fig. 11A) and oblique rows of ganoid scales. The posterior location of the dorsal and anal fins reflects the feeding strategy of gars as ambush predators. Wiley (1976) has divided recent and fossil gars (first known from the Cretaceous) into two genera: *Lepisosteus* (4 fossil species, 4 living) and *Atractosteus* (5 fossil species, 3 living). Although fossil gars are known from North America, Europe, Africa, and India, the living gar species are restricted in distribution to North America where they generally inhabit rivers, streams, and lakes, although some species also live in brackish or occasionally marine waters. Gars have a bilobed lung that arises from a dorsal pharyngeal diverticulum and frequently take air from the surface which is pumped into the lung. The lung is similar to that in the living halecomorph *Amia* in having a highly subdivided interior to increase respiratory surface area (Rahn *et al.*, 1971). The largest living gar, *Atractosteus spatula*, the alligator gar, has been reported to reach a length of over 3 meters and occurs in brackish water along the Gulf of Mexico and in the Mississippi River.

The extinct family Semionotidae (Fig. 6) includes about 20 genera of fishes. Until recently the gars were grouped with the semionotid fishes in the order Semionotiformes, but as discussed above they now constitute a separate division, the remaining forms comprising the family Semionotidae within the division Halecostomi. While the semionotids may well represent an unnatural assemblage of fishes grouped together only because they share certain general similarities (many of the genera are known only from extremely poor fossils, Patterson, 1973) the majority share two characters of fundamental importance with the Halecomorphi and Teleostei: the presence of a mobile maxillary bone in the cheek and an interopercular bone (Fig. 6: characters 14 and 15), thus placing them in a more cladistically derived position than the gars.

Figure 13 depicts the major musculoskeletal elements in the head of a primitive teleost and how they interact during prey capture. This same basic system is present in amiids and halecomorphs (with the exception of the geniohyoideus muscle, see below). The evolution of a separate interopercular bone (Fig. 13: iop) allowed a new system of muscles and bones to activate opening of the mouth. Contraction of the levator operculi muscle rotates the opercular bone dorsally (Fig. 13: lo, op) and this force is transmitted via the interopercular bone and ligament l_1 to the lower jaw causing it to move ventrally and open the mouth. This mechanism for opening the mouth evolved at the halecostome level (Lauder, 1980c). The primitive actinopterygian mechanism for depressing the lower jaw in-

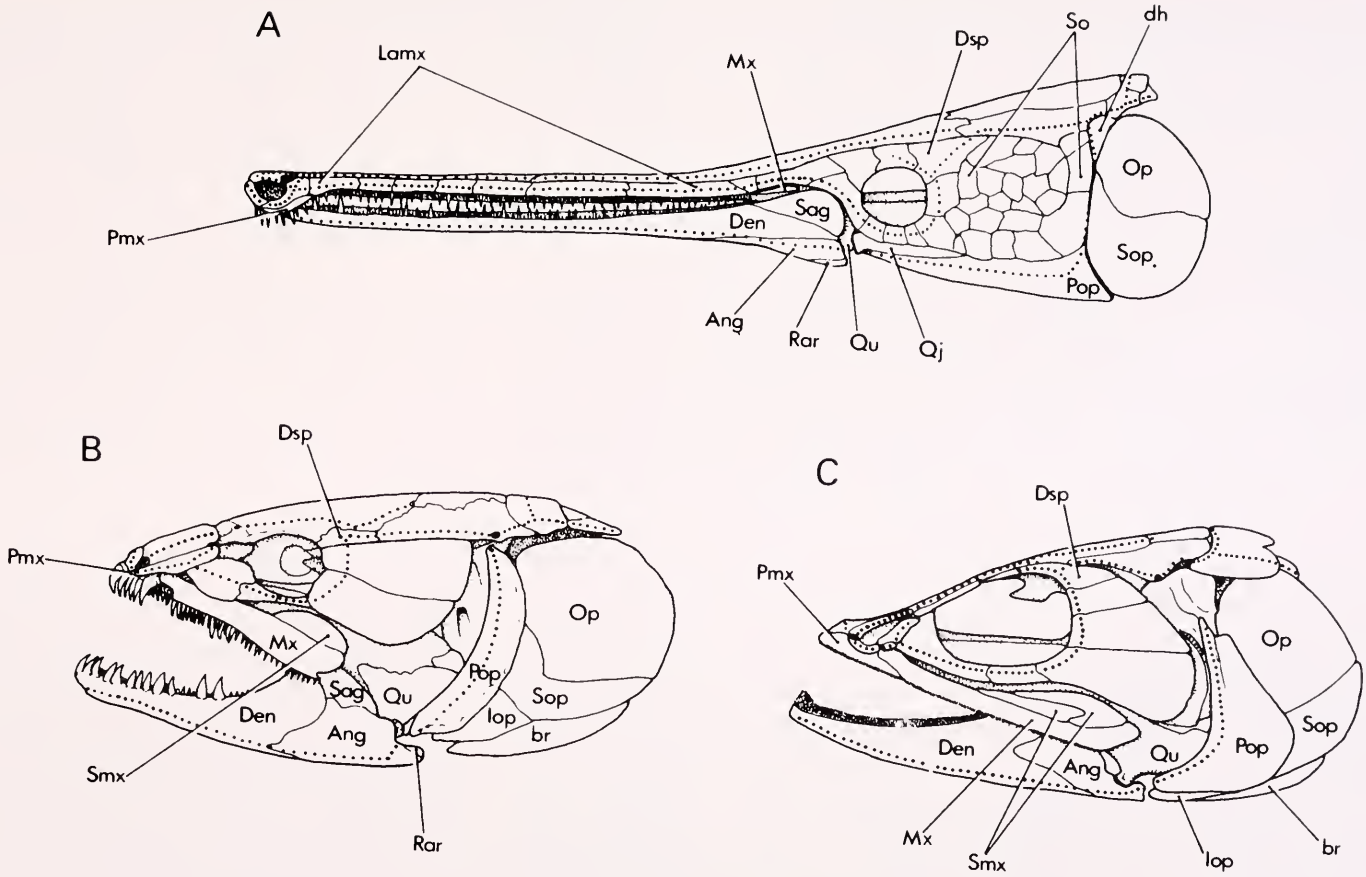


Figure 12. Lateral views of the skull of A, *Lepisosteus platostomus*, a ginglymod; B, *Amia calva*, a halecomorph; C, *Elops saurus*, a primitive teleost (Elopomorpha). Dotted lines denote the course of the sensory canals. (From Patterson [1973]), reprinted by permission of the Council of the Linnean Society of London.)

Abbreviations: Ang, angular; br, branchiostegal rays; Den, dentary; Dsp, dermosphenotic; Iop, interoperculum; Lamx, infraorbital bones; Mx, maxilla; Op, opercle; Pmx, premaxilla; Pop, preoperculum; Qj, quadratojugal; Qu, quadrate; Rar, retroarticular; Sag, surangular; Smx, supramaxilla; So, suborbitals; Sop, suboperculum.

volves posterior movements of the hyoid arch caused by contraction of the sternohyoideus and hypaxial (obliquus inferioris) muscles and the transmission of this movement by ligament 1_2 (Fig. 13: hyoid, $\dot{s}h$, 1_2) to the lower jaw. This last mechanism was present in paleoniscoids and is also found in *Polypterus, Lepisosteus*, halecomorphs, and many primitive teleosts. Use of the sternohyoideus, ventral body muscles, and the mandibulohyoid ligament as a system mediating mouth opening may in fact be primitive for gnathostomes, as the requisite anatomical features and mechanical relationships are found in elasmobranchs, coelacanths, and lungfishes, as well as in primitive rayfinned fishes. The salient specialization of the halecostome feeding mechanism is thus the occurrence of two biomechanical pathways controlling lower jaw depression. The presence of a maxillary bone that has been freed from the cheek (in contrast to the primitive actinopterygian condition; compare Figs. 12 and 13 to Fig. 8) contributes to the suction feeding mechanism since during mouth opening the maxilla swings towards the prey and creates a "tunnel" which directs water flow from the region immediately in front of the mouth into the buccal cavity (Lauder, 1979). The importance of the interopercular bone and the free maxilla is that they indicate the presence in the "semionotids," halecomorphs, and primitive teleost fishes of a suction feeding mechanism similar in all key features to that of higher teleosts. This mechanism has been slightly modified in advanced teleosts, but prey capture by inertial suction feeding was clearly present in the early halecostome fishes.

The halecomorph fishes (Fig. 6), all extinct except for the living *Amia calva* (Fig. 11B), are united by the possession of a unique jaw articulation: both the quadrate and the symplectic contribute to the jaw joint. The main fossil taxa included in the Halecomorphi are the Parasemionotidae and the Caturidae, almost certainly paraphyletic groups (Patterson, 1973). The main lineage of interest, however, to students of extant organisms is the Family Amiidae (Fig. 6) containing *Amia calva*, the bowfin. Although the Amiidae has an extensive fossil record beginning in the Jurassic and covering Europe, Asia, and North America (Boreske, 1974), the family today is confined to North America. *Amia* inhabits freshwaters of the south and midwest up through the Mississippi drainage, into the Great Lakes (except Lake Superior) and reaches down into Lake Champlain in the east. Its common name, bowfin, derives from the elongate dorsal fin (Fig. 11B) which is undulated in a bowlike fashion during slow locomotion. *Amia* is a voracious predator, often consuming large numbers of prey in a short time, and exhibits the main characteristics of the halecostome feeding mechanism outlined above. In *Amia* the maxilla may achieve a nearly vertical position during the strike at the prey and high-speed movies of feeding sequences show that this contributes significantly to suction efficiency by creating a tunnel-like mouth opening. The bowfin is also able to breathe air and possesses a lung that arises as a dorsal diverticulum of the pharynx in a similar fashion to the lung of the gar, *Lepisosteus*. *Amia* reaches a maximum length of about one meter.

THE TELEOSTEI

The Early Teleost Fishes

The Teleostei comprise by far the most diverse group of Actinopterygii and, with an estimated 20,000 species (Cohen, 1970), far exceed the diversity of any other vertebrate group. The various subgroups of the Teleostei will be treated in the remainder of this paper. Teleosts are first known from the Middle Triassic, and for most of this century it has been thought that the Teleostei form an unnatural assemblage derived polyphyletically by many independent lin-

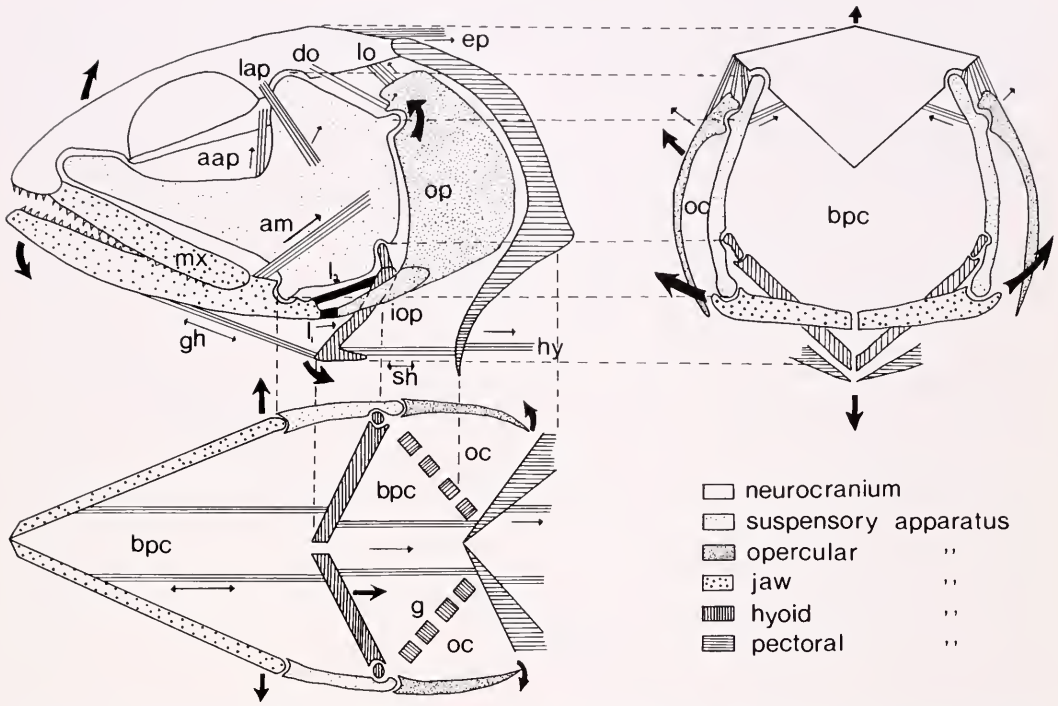


Figure 13. Diagrammatic model of the feeding apparatus in primitive teleost fishes. The major mechanical units of the jaw are shown in different patterns (see key). Heavy arrows indicate the major movements of the bony elements during mouth opening, light arrows indicate the major action of the muscles. (Modified from Lauder and Liem, 1980.)

Abbreviations: aap, adductor arcus palatini muscle; am, adductor mandibulae musculature; bpc, buccopharyngeal cavity; do, dilator operculi muscle; ep, epaxial muscles; g, gills; gh, geniohyoideus muscle; hy, hypaxial muscles; iop, interopercular bone; l_1, interoperculomandibular ligament; l_2, mandibulohyoid ligament; lap, levator arcus palatini muscle; lo, levator operculi muscle; mx, maxilla; oc, opercular chamber; op, operculum; sh, sternohyoideus muscle.

eages from the so-called pholidophorid fishes (Gosline, 1965; Patterson, 1967). Patterson (1968a) first proposed a precise definition of the Teleostei based on the anatomy of the caudal fin and showed that teleosts, as he defined them, do in fact constitute a natural, monophyletic assemblage of fishes which includes several groups previously thought not to be teleosts. The groups currently included in the Teleostei and their interrelationships are summarized in Fig. 14. Teleosts possess a caudal skeleton which differs from that of other neopterygian fishes (Rosen, 1982; Fig. 14: character 1) and is of key significance in the evolution of actinopterygian locomotor patterns. In haleco-

morph and ginglymod fishes (Fig. 15A, B) the caudal fin rays articulate with the posterior edge of the haemal spines and with flattened and expanded haemal arches and spines known as hypurals (Fig. 15: h1–h7). The caudal fin is heterocercal and is both internally asymmetrical (the vertebral column bends dorsally in the tail) and externally asymmetrical. A "chondrostean hinge" occurs at the base of the upper lobe of the primitive actinopterygian tail and represents a zone of weakness between the body scale rows (running in an obliquely posterior direction) and the scale rows in the epichordal tail lobe (with an anteroventral inclination) which serve to stiffen the tail (*Ad-*

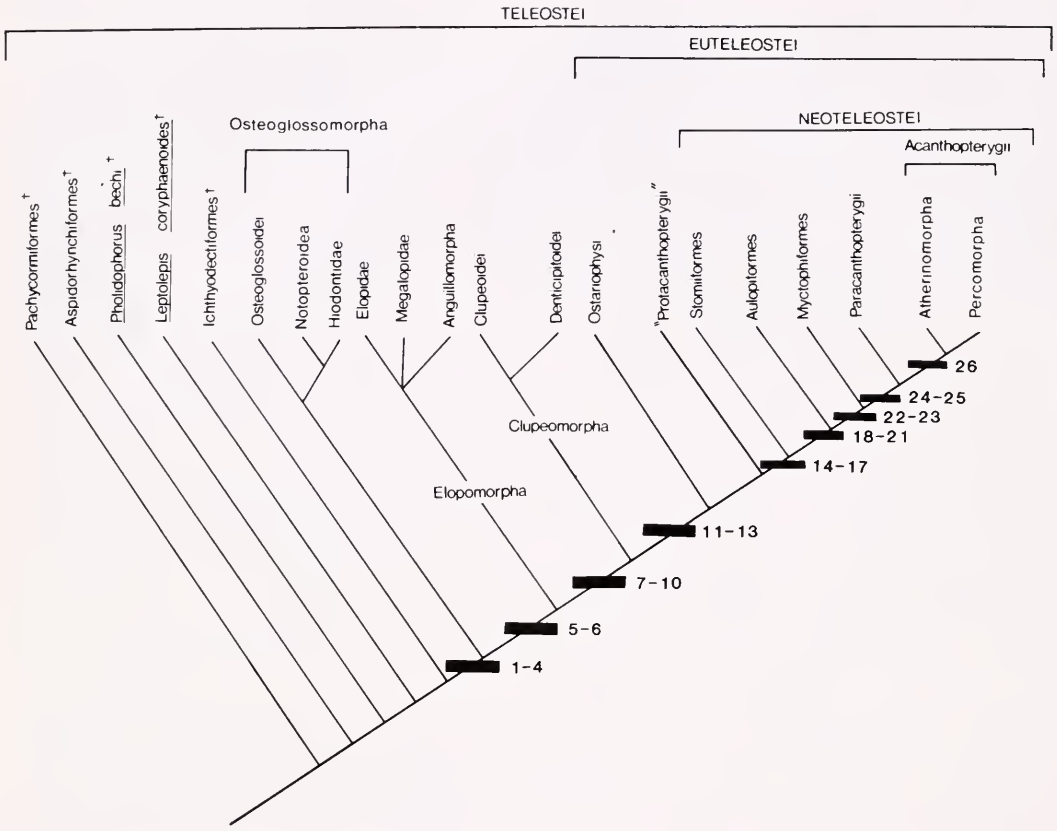


Figure 14. Phylogeny of the Teleostei. Taxa known only from fossils are indicated with a dagger. Monophyly of the Teleostei is established in Figure 6, and monophyly of the various subgroups is considered below. The "Protacanthopterygii" is discussed on p. 132, see Fig. 28. Characters corroborating the branching of the primitive teleostean fossil taxa are discussed and presented in Patterson (1977b). The characters are: **1,** presence of an endoskeletal basihyal (Nelson, 1969a; Patterson, 1977a); **2,** four pharyngobranchials; **3,** three hypobranchials present; **4,** basibranchial and basihyal cartilages overlain by median toothplates (Rosen, 1982); **5,** two uroneurals extend anteriorly over the second ural centrum (Patterson, 1977); **6,** "epipleural intermuscular bones developed throughout the abdominal and anterior caudal regions" (Patterson, 1977b: 630); **7,** retroarticular bone excluded from the quadratomandibular joint surface; **8,** toothplates fused with endoskeletal gill arch elements; **9,** neural arch on ural centrum one reduced or absent (Patterson, 1977b); **10,** articular bone co-ossified with the angular (Nelson, 1973); **11,** the presence of an adipose fin; **12,** presence of nuptial tubercles (Wiley and Collette, 1970); **13,** the presence of an anterior membraneous outgrowth of the first uroneural that does not meet its antimere in the midline (Patterson and Rosen, 1977); **14,** the presence of a retractor dorsalis muscle (see text; Rosen, 1973); **15,** a rostral cartilage (Fink and Weitzman, 1981); **16,** tooth attachment to bone is Type 4 (Fink, 1981); **17,** Aw division of adductor mandibulae has a posterior tendinous insertion on the quadrate, preoperculum, or operculum (Lauder, unpublished); **18,** reduction of second preural neural spine to a half-spine (Rosen, 1973); **19,** retractor dorsalis with a tendinous insertion on the third pharyngobranchial (Rosen, 1973); **20,** loss of the primitive mandibulohyoid ligament and the presence instead of an interoperculo-hyoid ligament (Lauder, 1982a); **21,** fusion of a toothplate to the third epibranchial. (Rosen (1973) lists several additional characters at this level, but these have been studied in more detail by Fink and Weitzman (1981) and are not found to be uniquely derived features); **22,** pharyngohyoideus (the primitive teleostean rectus communis) inserts on the urohyal, but see text for discussion (Lauder, 1982a); **23,** reduction or loss of pharyngobranchial four and the main insertion of the retractor dorsalis onto the third pharyngobranchial; **24,** the presence of well-developed ctenoid scales (Rosen, 1973; ctenoid scales, however, are also present in more primitive clades); **25,** expansion of ascending and articular premaxillary processes (Rosen, 1973; this level on the cladogram is not well defined); **26,** insertion of the retractor dorsalis onto the third pharyngobranchial only, and enlargement of epibranchials two and three. Various other features of the upper jaw mechanism are discussed by Rosen (1973, 1982) but none are unique to the Acanthopterygii and this group remains poorly defined. (But see character 1, Fig. 47, and Rosen and Parenti, 1981.)

uella, Fig. 7C, shows this well; an arrow points to the hinge). This asymmetrically shaped tail is presumed to generate an asymmetrical thrust with respect to the body axis.

In teleosts, however, the ural neural arches have become elongated into uroneurals (Fig. 15C: un 1–3) which function both to stiffen the upper tail lobe and to support a series of dorsal fin rays (Fig. 15C: epr). The hypurals have become expanded, and the net result is an internally asymmetrical but externally symmetrical caudal fin. In the earliest teleost fishes the uroneurals were rather small and dorsal fin rays were tightly bound to the dorsal hypurals to stiffen the upper lobe. In most teleosts, the uroneurals extend far anteriorly across the first and second preural centra (Fig. 15C: un 1–3) and completely eliminate the primitive line of flexion in the upper tail lobe. The functional significance of the anatomical changes in caudal structure for teleostean locomotion remains problematical. It is usually assumed that the externally symmetrical teleostean tail generates symmetrical thrust that passes through the center of mass of the fish, in contrast to the oblique (anteroventral) thrust generated by the asymmetrical chondrostean tail (Patterson, 1968a). There is, however, very little experimental evidence to support such speculations, and all of the detailed experimental studies on caudal structure and function (e.g., Webb, 1975, 1982) have focused on euteleostean fishes. The first actual measurements of bone deformations in the symmetrical tail of teleost fishes (Lauder, 1982b; see Fig. 16) show that during continuous locomotion, the hypurals are probably being twisted about their long axis, and that the thrust may be anteroventrally inclined. During rapid fast-start accelerations, however, strain patterns are consistent with an anteriorly directed thrust (Fig. 16). These data underscore the need for caution in simple extrapolations ("symmetrical tail equals symmetrical thrust") and the necessity for comparative functional data from living non-teleost actinopterygians such as *Amia*, *Lepisosteus*, and *Polypterus*. The oft-cited correlation between the reduction in weight of scalation, increased buoyancy control, and symmetry of caudal structure needs to be subjected to critical examination.

Teleost fishes may also be characterized by modifications in the jaw musculature. Non-teleost actinopterygians are all very similar in ventral throat musculature anatomy, closely resembling the primitive condition illustrated in Figure 8 with an intermandibularis posterior muscle spanning the mandibular rami, and an interhyoideus extending anteriorly from the ceratohyal and epihyal to insert on the branchiostegal rays and fascia dorsal to the gular plate(s) and intermandibularis posterior. In teleosts, the geniohyoideus muscle extends between the mandibular symphysis and the hyoid (Fig. 13: gh) and is composed of a fused intermandibularis posterior (trigeminal innervation) which forms the geniohyoideus anterior, and the interhyoideus (facial innervation) which comprises the geniohyoideus posterior (see Winterbottom, 1974a). The hyohyoideus musculature of teleosts, which regulates abduction and adduction of the branchiostegal rays and is instrumental in governing branchiostegal pump function during respiration (Gosline, 1971), appears to be derived from the interhyoideus of primitive actinopterygians. Finally, teleost fishes have lost the anterior component of the adductor mandibulae present in primitive actinopterygians (Fig. 8: AMa), and also in *Amia* as the "levator maxillae superioris" (Allis, 1897).

Teleostean phylogeny has been the subject of intensive investigation in the last decade, stimulated primarily by the publication in 1966 of the now classic paper by P. H. Greenwood *et al.* on teleostean phylogeny and classification. Prior

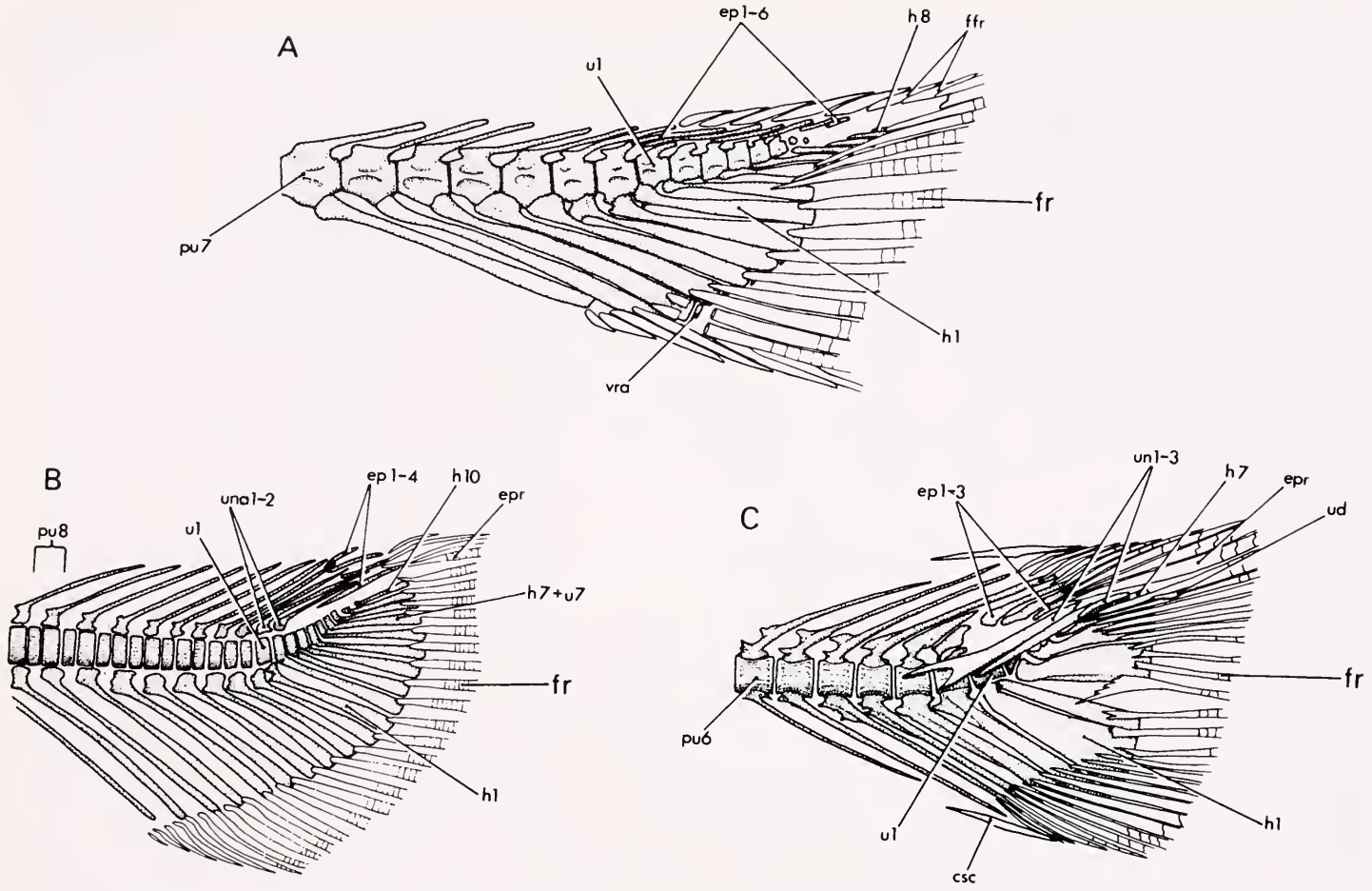


Figure 15. Caudal skeleton. A. A ginglymod (*Lepisosteus osseus*). B. A halecomorph (*Amia calva*). C. A teleost (*Elops saurus*). See text for discussion. (After Patterson [1973], reprinted by permission of the Council of the Linnean Society of London.)

Abbreviations: csc, caudal scute; ep, epurals; epr, lowermost epaxial fin ray; fr, fin ray; ffr, fringing fulcra; h, hypural, pu, pre-ural centrum; u, ural centrum; ud urodermal; un, uroneural; una, ural neural arch, vra, ventral caudal radial.

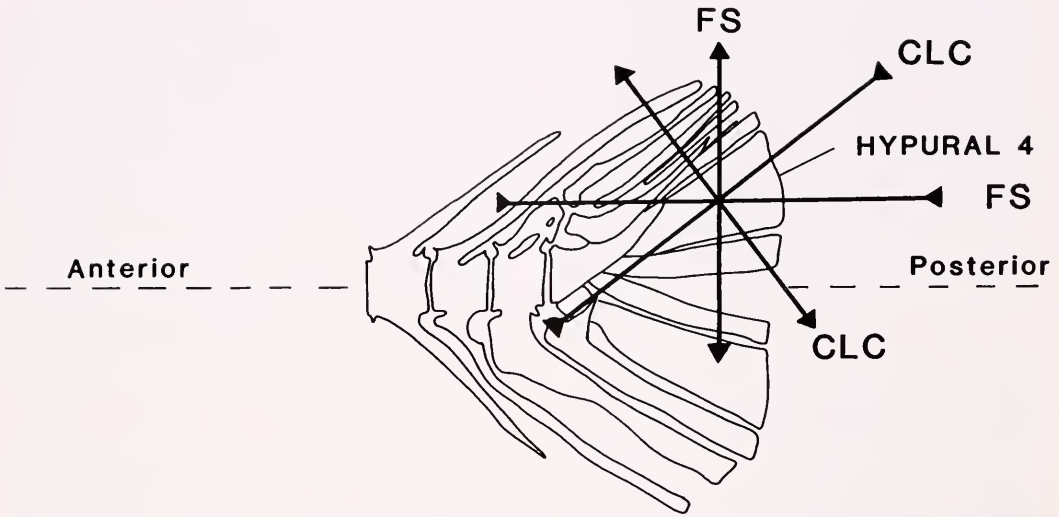


Figure 16. Caudal skeleton of a pumpkinseed sunfish (*Lepomis gibbosus*) showing the patterns of hypural compression and tension resulting from both continuous locomotion (CLC) and fast-start accelerations (FS). Hypural deformation was recorded with a strain gauge (see Lauder, 1982b). Note that during continuous locomotion the angle of the principal strain axes is tilted anteroventrally indicating that the hypurals are being twisted. There is no necessary correlation between the presence of an externally symmetrical tail and symmetrical patterns of thrust or deformation.

to 1966, views on the interrelationships of the major groups of living fishes had changed little since the work of C. T. Regan in the 1920's and teleostean phylogeny was poorly understood. Patterson (1977b: 634) has noted that "the mammalian analogy would be if the distinction between monotremes, marsupials, and placentals was not recognized until ten years ago." Greenwood *et al.* (1966) dismantled many of the clearly unnatural groups of teleost fishes, and the subsequent impact of the methodology of Hennig (1966) has resulted in a tremendous increase in our understanding of teleostean phylogeny (see Greenwood *et al.*, 1973; Patterson and Rosen, 1977). Patterson and Rosen (1977) have recently reexamined several of the early fossil teleostean groups, in particular the pholidophorids, leptolepids, and ichthyodectids, and have concluded that only the ichthyodectiforms constitute a natural group (Fig. 14). Many of the fishes assigned to the "Pholidophoridae" and "Leptolepidae" are so poorly known that only a few forms can be placed with confidence (Fig. 14).

There are four major groups of living teleosteans, the Osteoglossomorpha, the Elopomorpha, the Clupeomorpha, and the Euteleostei; and while hypotheses of the interrelationships of these groups have changed considerably within the last decade, each appears to be a well corroborated monophyletic group. Each of these groups will be considered in detail below. The interrelationships of the four major living groups of teleosts have been most recently examined by Patterson and Rosen (1977) and their account is summarized in Fig. 14. The osteoglossomorph ("bony-tongued") fishes comprise the most primitive group of living teleosts (also see Gosline, 1980). The other three groups (elopocephalans) are united by the presence of only two uroneurals (Fig. 14: character 5). Gosline (1965; 1980: 21) has suggested that this group shares a nasal pumping system effected by movements of the antorbital bone, but this character has yet to be examined in de-

tail. Within the elopocephalan assemblage, the Elopomorpha (tarpons and eels) are the most primitive group. The more derived Clupeomorpha (herrings) and Euteleostei share several features of cranial and caudal anatomy (Fig. 14).

While the Euteleostei form the bulk of teleost fishes, this group has also been one of the most difficult to characterize with derived characters. Although three characters in particular are commonly used (Fig. 14: 11–13), these features are widely distributed only in primitive euteleostean fishes (many of which lack the characters) and do not form an entirely satisfactory definition of the group. A comprehensive defining set of characters for the Euteleostei remains a key goal of systematic ichthyology.

The feeding mechanism in the early teleost fishes, depicted diagrammatically in Figure 13, differs from both that of the early actinopterygian fishes and that of advanced teleosts with a protrusible upper jaw. The premaxilla is usually small and slightly mobile on the neurocranium although in some groups (e.g., the Osteoglossomorpha) it becomes immovably attached to it. The maxillary bone (Figs. 12 and 13: mx) forms the main tooth-bearing element of the upper jaw and swings anteriorly during prey capture to occlude the corners of the mouth. This system differs very little from the feeding mechanism of *Amia*. In general, the inertial suction feeding mechanism of teleost fishes involves expansion of the orobranchial chamber (Fig. 13: bpc) by elevation of the head, depression of the jaw, depression of the hyoid apparatus and lateral movements of the suspensory apparatus. These expansive movements create a low pressure center in the buccal cavity which creates a flow of water into the mouth. The inertial suction feeding mechanism is a feature of major significance to the evolution of teleostean fishes.

The Osteoglossomorpha

The osteoglossomorph fishes have been subjected to close scrutiny by systematic ichthyologists in recent years. Greenwood (1967, 1970, 1971, 1973), Nelson (1968, 1969b, 1972), and Taverne (1977, 1978, 1979) have conducted the most comprehensive analyses. Despite this literature, it is still not possible to show convincingly that osteoglossomorph fishes are strictly monophyletic. Although no recent author appears to have doubted this, other groups such as the ichthyodectiforms (Fig. 14) are often included in the Osteoglossomorpha (e.g., Taverne, 1979), and few of the characters proposed as corroborating monophyly stand up to close examination.

Osteoglossomorphs are first known from the Upper Jurassic, but the branching from the elopocephalan lineage (Fig. 14) may be considerably older than this. Of special interest to biogeographers is the fact that living or fossil osteoglossomorphs are known from every continent except Europe (Patterson, 1981a) and a new set of lycopterids, relatives of the living *Hiodon* (North American), have recently been reported from China.

Two characters are often mentioned as characteristic of osteoglossomorph fishes: the presence of a "tongue—parasphenoid bite," and paired bony rods or processes at the base of the second gill arch (see Lauder and Liem, in press; Greenwood, 1973; Nelson, 1968). The osteoglossomorph fishes take their name from the tongue bite in which the basihyal, covered by a massive toothplate, "bites" against the roof of the mouth which bears large teeth (Fig. 17). Nelson (1968: 271) has suggested that in mormyrids, the first basibranchial supports most of the tongue toothplate.) The biting action occurs following initial prey capture by inertial suction, and results in the shredding and decapitation of prey items. The utility of this chewing complex for characterizing the Osteoglossomorpha is called into question by the observation that *Heterotis* and *Gymnarchus* lack parasphenoid teeth, and that parasphenoid teeth are present in more primitive fossil teleostean clades (Patterson and Rosen, 1977;

Fig. 14). This chewing apparatus may thus be shared by more primitive teleost fishes and not be indicative of osteoglossomorph monophyly. All osteoglossomorphs do, however, appear to share an additional feature of the chewing complex. The palatal bones (mesopterygoid and ectopterygoid) are toothed (in *Heterotis* only the mesopterygoid is toothed), and as the basihyal teeth move dorsally to "bite" against the parasphenoid as a result of hyoid protraction, shearing of the prey occurs between the basihyal teeth and the lateral mesopterygoid and/or ectopterygoid teeth. This shearing action is thus in addition to the puncturing and crushing provided by the basihyal—parasphenoid bite, and the entire tongue-bite complex functions as a highly effective mechanism for immobilizing and preparing prey for digestion.

The second character often used to distinguish osteoglossomorph fishes is "the evolution of a discrete connection between the sternohyoid and the second gill arch near the midline" (Fig. 18; Greenwood, 1973: 309). An examination of sternohyoid—gill arch relationships in teleosts reveals that a widespread feature in elopomorphs, clupeomorphs, ostariophysans, paracanthopterygians, and many acanthopterygians is a tendinous connection between the sternohyoideus and a ventrally directed process on hypobranchial three (Lauder, 1983). This feature appears to be primitive at least for elopocephalans, although the possibility that ichthyodectids, *Pholidophorus*, or aspidorhynchiforms also possessed a sternohyoideus connection to the gill arches cannot be ruled out. However, the attachment of the sternohyoideus to hypobranchial *two* does appear to be confined to osteoglossomorphs. Most osteoglossomorphs have ventrally directed processes on both hypobranchials two and three, and unless this feature is found in more primitive fossil teleosteans it would seem to be unique to osteoglossomorph fishes.

One convincing character uniting all living osteoglossomorphs into a monophyletic group is the pattern of coiling in the gut (Nelson, 1972). In all primitive actinopterygians, "the anterior part of the intestine passes posteriorly to the right of the esophagus and stomach" (Nelson, 1972: 326), and this is true for higher teleosts as well. In osteoglossomorphs, the gut passes to the left of the esophagus and stomach, and one or two pyloric caeca are consistently present. A summary of the other characters that corroborate osteoglossomorph monophyly is presented in Figure 19.

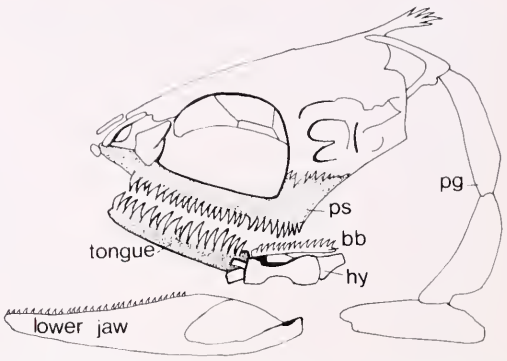


Figure 17. Lateral view of the syncranium, tongue, hyoid (hy), basibranchial (bb), lower jaw, and pectoral girdle (pg) of *Hiodon*, to show the major bony components of the "tongue-parasphenoid bite" which is common to many osteoglossomorph fishes. Note the massive dentition on the tongue and the parasphenoid (ps) of the roof of the mouth. Not shown are the toothed bones of the palatoquadrate located lateral to the tongue on each side. The shearing mechanism resulting from dorsoventral movements of the tongue with adducted palatoquadrates appears to be a shared feature of all osteoglossomorphs. More primitive teleosts have parasphenoid (and perhaps also basihyal) teeth and not all osteoglossomorphs possess a dentigerous parasphenoid.

Within the osteoglossomorpha, there is a great diversity in trophic biology. Insectivorous and piscivorous predators as well as filter feeders and benthic feeding fishes occur. *Heterotis*, a filter feeder, has a specialized epibranchial organ (Taverne, 1977; Nelson, 1967a) which apparently functions in the maceration of filtered material prior to swallowing. The gross morphology of the osteoglossomorph brain (Fig. 20) appears to be relatively primitive, although the forebrain of *Arapaima* and the enormously en-

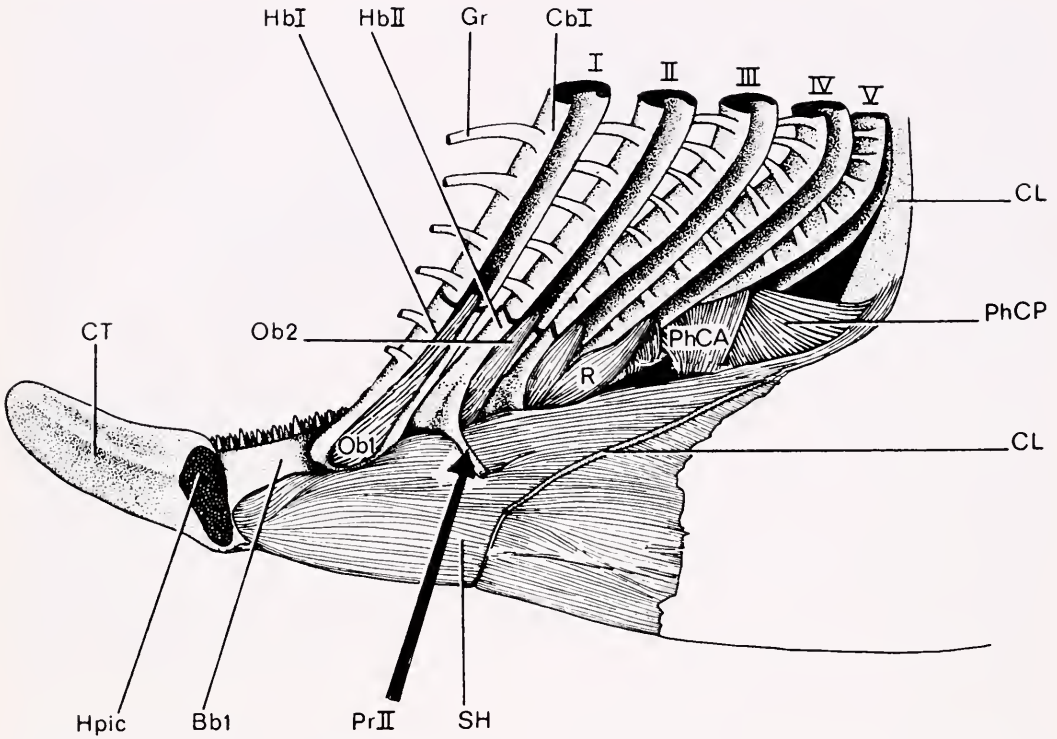


Figure 18. Ventral gill arch muscles and sternohyoideus (SH) of *Scleropages* in left lateral view (from Greenwood [1971], courtesy of the Trustees of the British Museum [Nat. Hist.]). The hypohyal has been partly cut away. Note the prominent bony process on the second gill arch indicated by the arrow.

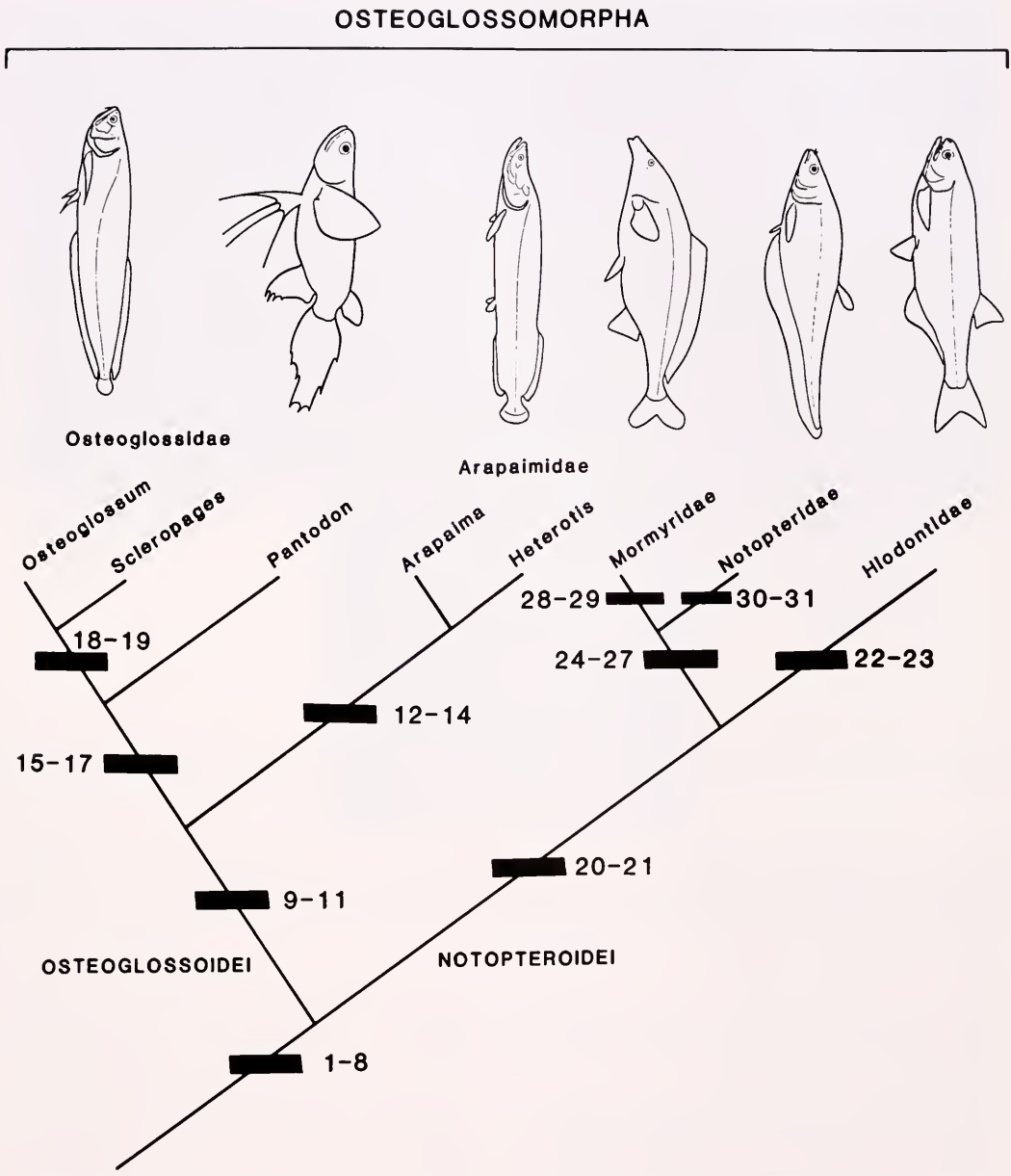
Abbreviations: Bbl, basibranchial one; Cb I–V, ceratobranchials (arches I–V); CL, cleithrum; CT, connective tissue surrounding lateral and ventral edges of basihyal and its anterior tooth plate; Gr, gill rakers; Hb I and II, hypobranchial of first and second arch; Hpic, hypohyal (cut through); Ob 1–3, obliquus muscle (1st–3rd gill arches), PhC A and P, external and internal pharyngocleithralis muscles; PRII, bony process from second hypobranchial; R, rectus muscle; SH, sternohyoideus muscle.

larged cerebellum of the electrogenic mormyrids clearly represent specialized conditions.

The Osteoglossomorpha may be divided into two major clades, the Notopteroidei, containing the families Notopteridae, Mormyridae, and Hiodontidae, and the Osteoglossoidei containing the Os-

→

Figure 19. Phylogenetic relationships of the Osteoglossomorpha. Characters are: **1,** "shearing bite" between the basihyal teeth and lateral pterygoquadrate teeth; **2,** small premaxilla firmly fixed to the skull; **3,** intestine coils to left of esophagus and stomach (Nelson, 1972); **4,** Taverne (1979) has recently proposed (but also see Gosline, 1960; Greenwood *et al.*, 1966) that osteoglossomorphs share a distinctive caudal skeleton in which one or more epurals are fused with neural arches of the caudal to form "neurepurals"; **6,** parapophyses fused with vertebral centra; **7,** loss of supramaxillae; **8,** other, more questionable characters proposed for the Osteoglossomorpha include reticulate scales, 16 or fewer branched caudal rays, and a ventral process at the base of the second gill arch (see text); **9,** fusion of hypurals (usually 3, 4, and 5 at least); **10,** septum bisecting the eye, extending between the retina and lens (Haedrich *et al.*, 1973); **11,** articulation between ventrolateral peg of the parasphenoid and the entopterygoid (Greenwood *et al.*, 1966: 363); **12,** fusion of antorbital and lacrimal (Nelson, 1969b); **13,** uroneurals fused with the dorsalmost hypural; **14,** third infrapharyngobranchial "with medial portion segmented off as a distinct cartilage" (Nelson, 1968: 268); **15,** maxilla fixed to cheek and does not swing anteriorly on its dorsal palatal articulation during feeding; **16,** small "A1" division of the adductor mandibulae inserts on the maxilla (personal observation; Kershaw, 1976); **17,** single basibranchial toothplate "extending



to the anterior end of a cartilagenous basihyal" (Nelson, 1968: 269) (see Taverne [1979] for numerous other characters); **18,** numerous unique features of the gill arches (Nelson, 1968) including the structure of the basibranchials and infrapharyngobranchials; **19,** loss of the orbitosphenoid (Greenwood *et al.,* 1966: 362) (see Taverne [1979] for numerous other characters); **20,** "osteoglossomorph type" of otophysic connection (see Greenwood, 1973); **21,** ventral throat musculature containing an anteroposteriorly oriented intermandibularis posterior muscle that is not fused with the interhyoideus; **22,** medial process of the second and third infrapharyngobranchials of each side overlapping in the midline (Nelson, 1968); **23,** uniquely specialized infraorbital bones (Nelson, 1969b); **24,** utriculus completely separated from the sacculus and lagena, **25,** lateral line without pores; **26,** brain with greatly enlarged cerebellum; **27,** dentary sensory canal is an open groove rather than enclosed (Nelson, 1973); **28,** cerebellum encloses most of the rest of the brain; **29,** well-developed electrogenic and electroreceptive capability (amongst many other unique features of this family); **30,** ventral hypohyal lacking; **31,** ventral bony scutes present. (Drawings of fishes from J. S. Nelson [1976], courtesy of John Wiley Publishing Co.)

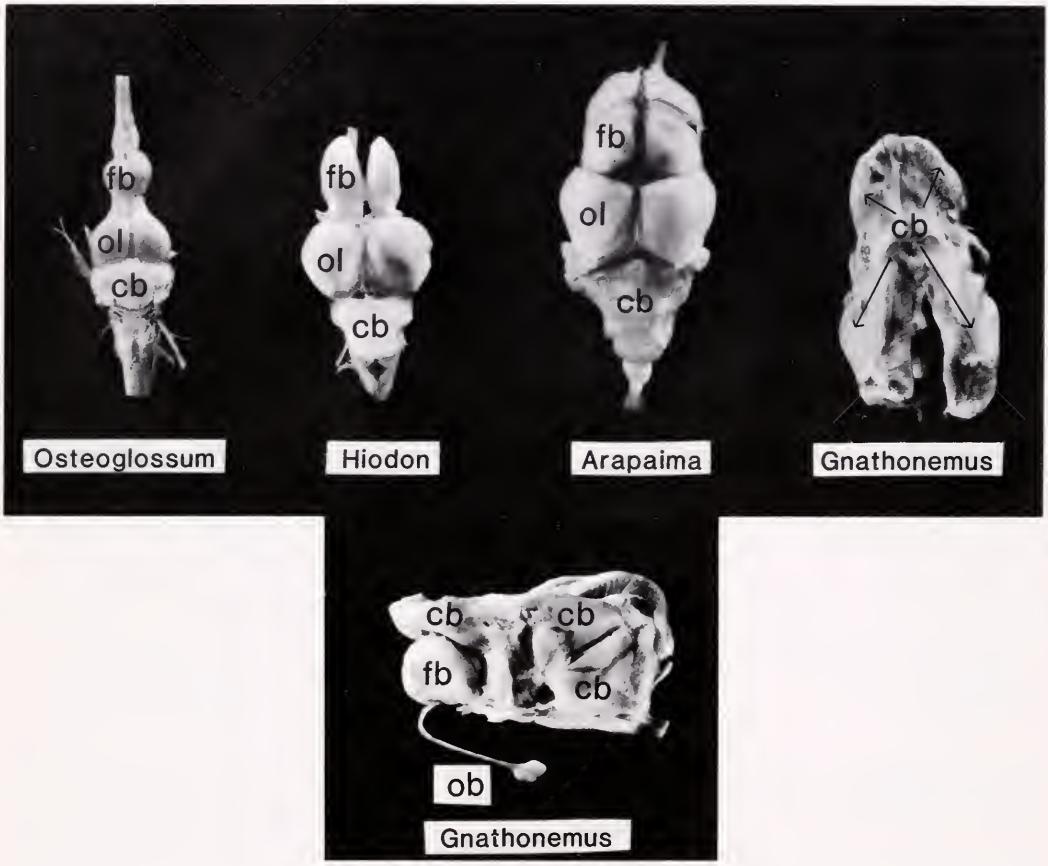


Figure 20. Dorsal views of the brains of some representative osteoglossomorphs. The cerebellum (cb) in *Osteoglossum* and *Hiodon* exhibits only a moderate increase in size. In *Arapaima* the cerebellum is enlarged as in most osteoglossomorphs. In *Gnathonemus* the cerebellum is greatly enlarged enveloping the rest of the brain.

Abbreviations: cb, cerebellum; fb, forebrain; ob, olfactory bulb; ol, optic lobe.

teoglossidae and *Arapaima* and *Heterotis*, here united into the Arapaimidae (Fig. 19).

Osteoglossoidei. Members of this clade possess one muscle, the geniohyoideus, extending between the mandible and the hyoid (Fig. 21A) (Greenwood, 1973; Kershaw, 1976). Although this character has been used as a shared derived feature for this group, the presence of a single geniohyoideus muscle is primitive for teleosts (Lauder, 1982a; see p. 117) and is not indicative of shared common ancestry. Most members of this group possess so-called reticulate scales (Fig. 22) with small surface ridges ("circulae") aligned concentrically in a semicircle on the distal exposed aspect of the scale (see Nelson, 1969b: 24, 25; Taverne, 1979: 70). Reticulate scales are also found in the mormyrids as well as in several other teleosts.

Osteoglossum, Arapaima, Scleropages, and *Heterotis* have evolved a mouthbrooding behavior for caring for the young, and this pattern of parental care appears to be primitive for the Osteoglossoidei. *Pantodon,* a highly specialized member of this group, is a small surface-dwelling fish with an upturned

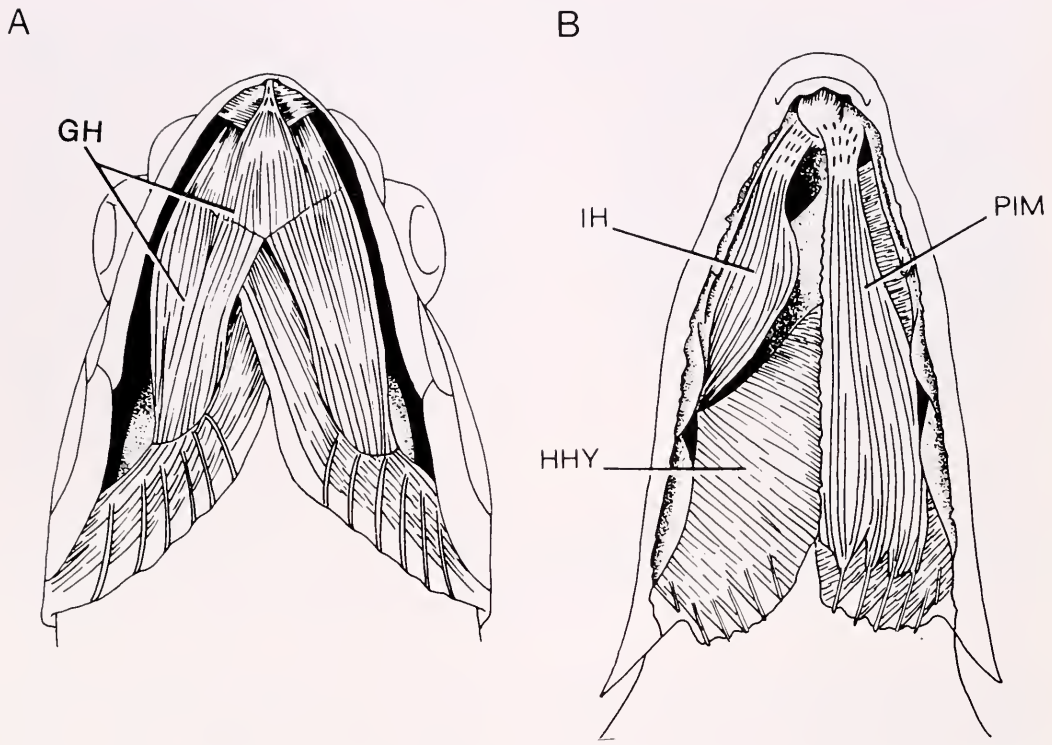


Figure 21. A. Ventral hyoid musculature of an osteoglossoid (*Pantodon*) showing the single muscle, the geniohyoideus (GH) between the mandible and the hyoid. B. Ventral hyoid musculature of a mormyrid (*Mormyrus*), showing the two muscles, the interhyoideus (IH) and posterior intermandibularis (PIM), between the mandible and the hyoid (From Greenwood [1971], courtesy of the Trustees of the British Museum [Nat. Hist.].)

mouth. Prey are small insects caught in the surface film, and *Pantodon* also breathes highly oxygenated water from just below the surface. It has been suggested that *Pantodon* is capable of air-breathing, a behavior well documented in *Arapaima* which uses a modified swimbladder as a lung.

Notopteroidei. The ventral throat musculature in the three clades comprising this suborder is distinctly modified (Fig. 21B). *Hiodon* shows the most generalized condition while mormyrids and notopterids show a specialized interhyoideus and posterior intermandibularis that is clearly a derived condition. The inner ear of mormyrids and the notopterid knife fishes shares a condition in which the utriculus and its semicircular canals are completely separated from the sacculus and lagena (Fig. 23), and the highly specialized cephalic lateral line system is without pores. The family Notopteridae possesses an enlarged toothplate covering the tongue and an enlarged cerebellum. Notopterids are elongate and laterally flattened nocturnal fishes that propel themselves by undulations of the long anal fin and are capable of breathing air. Unlike the other osteoglossiform families which have very few species, the Mormyridae has undergone an evolutionary radiation differentiating into over 300 species. The most outstanding features characterizing this family are the electrogenic organs derived from caudal muscles and the greatly enlarged cerebellum (Fig. 20). Mormyrids feed at least in part by electrolocation (Hopkins, 1981) and exploit the rich bottom fauna of small

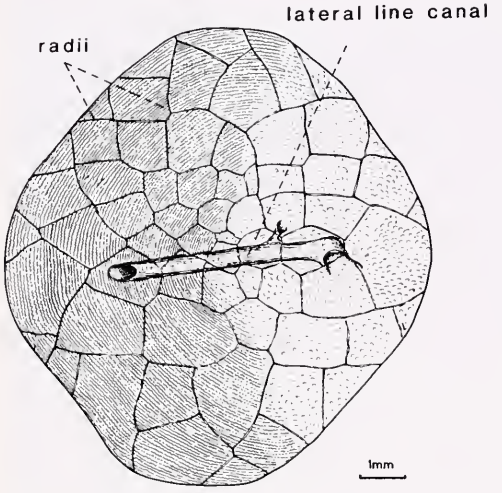


Figure 22. Lateral line scale of *Osteoglossum bicirrhosum*. The scale is typically ornamented. The radii form a coarse and irregularly reticulated pattern, both apically and basally. (After Taverne, 1977.)

worms and wormlike insects. The mormyrids largely occupy nocturnal bottom feeding niches in the rivers of Africa. *Gymnarchus niloticus*, often placed in a separate family Gymnarchidae, is a close relative of the mormyrid fishes.

The last clade in the Notopteroidei is the genus *Hiodon*, with two extant species, *Hiodon tergisus* and *H. alosoides*. These are the only osteoglossomorphs found in North American waters. Although *Hiodon* is often cited as being a very primitive teleost, it shows many specializations, especially in the braincase and swimbladder (Greenwood, 1973). The swimbladder has a diverticulum on each side extending anteriorly into the ear. Within the ear, this diverticulum is separated by a thin membrane from a vesicle which is filled with perilymph and connected with the utriculus of the inner ear via a foramen in the prootic bone.

The Elopomorpha

The Elopomorpha contains about 650 species (J. Nelson, 1976) which vary tremendously in body form and habit from the more conventionally shaped megalopids (tarpons) to the highly aberrant saccopharyngoid deepsea eels. Elopomorph fishes may be divided into seven major groups: the Elopidae, tenpounders; the Megalopidae, tarpons; the Albulidae, bonefishes; the anguilloids, eels, containing about 600 of the 650 elopomorph species and about 19 families; the saccopharyngoids, bathypelagic eels; the Halosauridae, deep-sea halosaurs; and the Notacanthidae, deep-sea spring eels.

The interrelationships of these groups has been a matter of considerable debate in recent years, and elopomorph phylogeny has been most recently considered by Greenwood (1977) and Patterson and Rosen (1977). It has become increasingly clear, however, that the elopomorph fishes form a natural, monophyletic group which may be defined on the basis of several specializations (Forey, 1973a, b; Greenwood, 1977; Patterson and Rosen, 1977). The most remarkable feature shared by elopomorph fishes is the occurrence of a leptocephalus larva, an elongate ribbonlike larva with a small head and greatly extended body. See Hulet (1978) and Leiby (1981) for descriptions of eel leptocephali. The leptocephalus may be larger than the adult and is generally translucent with clearly visible segmented myotomes along the body. While the larval forms of all elopomorphs are not known, leptocephalus larvae do occur in all of the major elopomorph groups. A number of osteological features also may be used to define the Elopomorpha (Fig. 24): fusion of the angular and retroarticular bones of the lower jaw and the occurrence of rostral and prenasal ossicles in the snout.

The Suborder Anguilloidei contains the vast majority of the elopomorph fishes and is divided into two superfamilies, the Anguilloidea and Saccopharyngoidea (Fig. 24). The saccopharyngoids, with eight nominal species in three families, are highly specialized deep-sea fishes with elongate bodies and large mouths capable of engulfing extremely large prey rel-

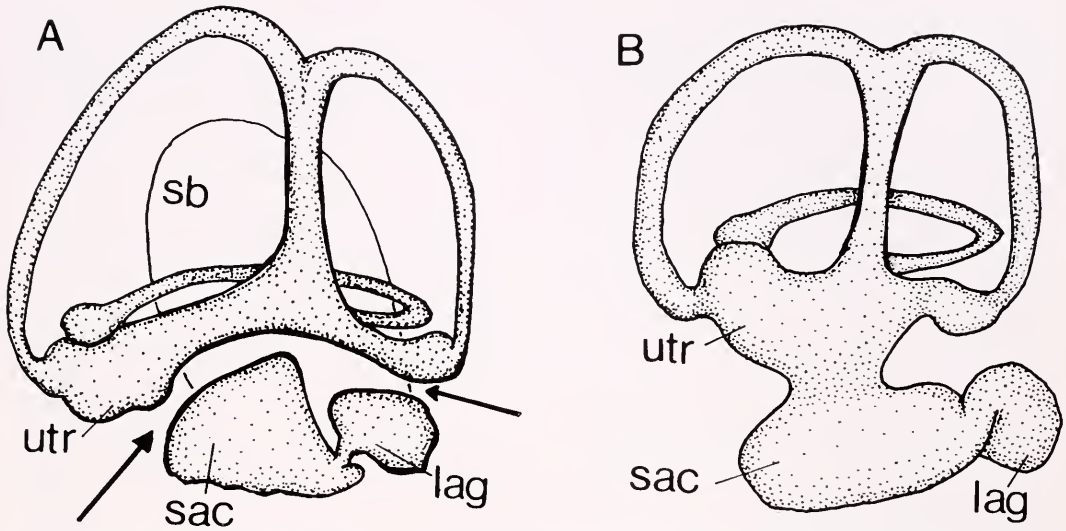


Figure 23. A. Medial view of the inner ear of a notopteroid, showing the complete separation of the utriculus (utr) with its semicircular canals from the sacculus (sac) and lagena (lag). The intraotic extension of the swimbladder (sb) is outlined. B. Medial view of the inner ear of an osteoglossoid exhibiting the primitive condition.

ative to their own body size. The skull is highly modified, and many bones are lacking as are scales, pelvic fins, the caudal fin, ribs, and swimbladder. These fishes are so bizarre that their relationships have been a matter of controversy in the past, although now it is generally recognized that the anguilloid eels are their closest relatives (Fig. 24). The Anguilloidea includes a wide diversity of eel-like fishes ranging from the well-known *Anguilla rostrata*, the American eel (Family Anguillidae), to the deep-sea snipe eels (family Nemichthyidae) and snake eels (Ophichthidae). All forms are highly elongate, and pelvic fins are absent in all Recent eels. The Anguillidae is the only family of eels containing members that spend part of their life in freshwater. All other eel families are exclusively marine. Spawning of the North American eel and the European eel (*A. anguilla*) takes place in the Sargasso Sea, and the leptocephalus larvae then drift either to North America or Europe where they metamorphose into elvers which often enter freshwater to mature into adults. The lifecycle is completed when the adults migrate back into the sea and travel to the Sargasso where reproduction occurs and the adults die. The American eel differs from the European species in spawning site as well as in the length of larval life. Both have the same pattern of life history.

The sister group of the Anguilloidei is a group, the Albuloidei, composed of the Albuloidea (bonefishes) and Halosauroidea (halosaurs and notacanths) (Fig. 24). The bonefishes, of which *Albula vulpes* is the best known, occur worldwide in tropical seas. They have a small mouth, and generally feed in schools on bottom living invertebrates. The halosauroids are divided into two groups, both found in the deep-sea with a worldwide distribution. The Halosauridae (3 genera) are elongate with a prominent lateral line and have a sensitive snout that is apparently used for food detection. Halosaurs are bathypelagic and retain a swimbladder (lost in many benthic fishes). The Notacanthidae, or spiny eels (Fig. 24), are similar in habit to the halosaurs although their

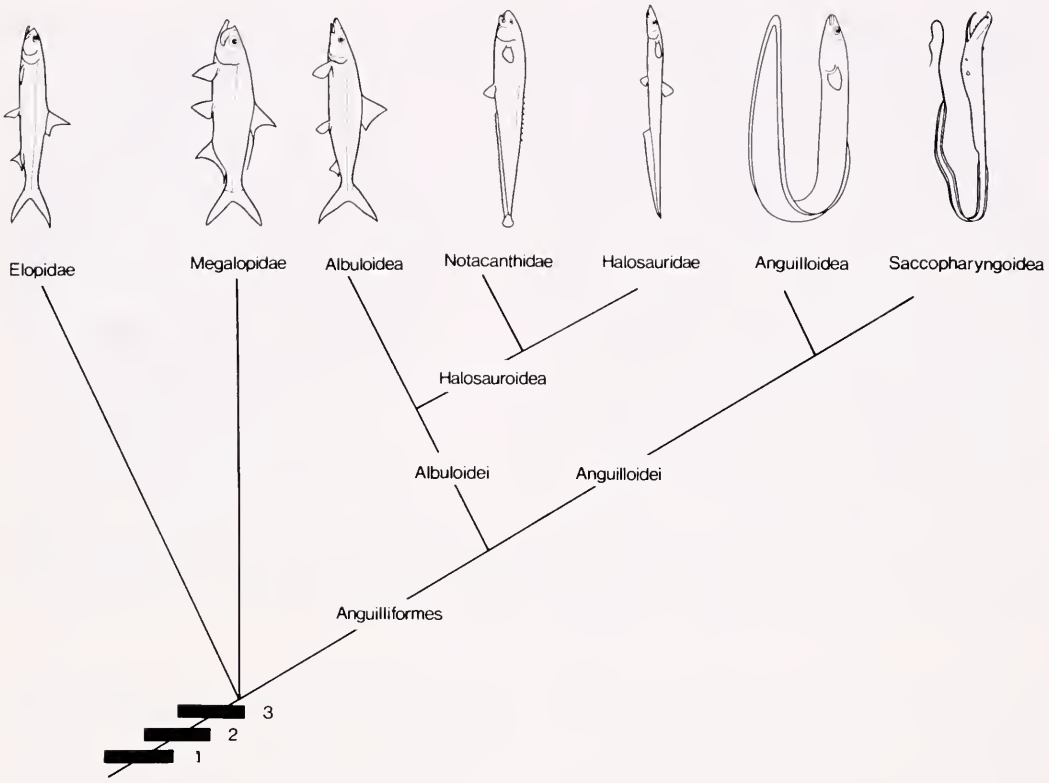


Figure 24. Phylogeny of the Elopomorpha. The Elopidae, Megalopidae, and Anguilliformes form an unresolved trichotomy based on present data. Shared derived characters of the Elopomorpha include **1,** the presence of a leptocephalus larva; **2,** fusion of the angular and retroarticular bones of the lower jaw; and **3,** the presence of rostral and prenasal ossicles. See Patterson and Rosen (1977) for further characters. Justification of the branching pattern in the Anguilliformes may be found in Greenwood (1977) and Forey (1973). (Drawings of fishes from J. S. Nelson [1976], courtesy of John Wiley Publishing Co.)

food seems to consist more of soft-bodied deep-sea invertebrates. One rather modified notacanth, *Lipogenys*, often placed in a separate family, is poorly known but lacks teeth and possesses a small subterminal suctorial mouth (Greenwood, 1977).

The two remaining groups of elopomorphs, the Megalopidae and Elopidae, are often considered to be closely related to each other, together forming the sister group to the Anguilliformes. Patterson and Rosen (1977) have recently reviewed the evidence for this dichotomy and have concluded that little justification exists, and, on present evidence, the interrelationships of the Elopidae, Megalopidae, and Anguilliformes are best represented as an unresolved trichotomy (Fig. 24). The family Elopidae, tenpounders, contains a single genus *Elops* with about five species which are distributed worldwide in tropical seas. Most commonly found in estuaries and near shore as adults, tenpounders may invade brackish waters. The Megalopidae, tarpons, with two species in tropical and subtropical waters of the Pacific and Atlantic, grow to a large size (maximum length about 2 m) and are unique among elopomorphs in possessing a connection between the ear and the swimbladder (Greenwood, 1970). This otophysic connection consists of paired

cranial swimbladder diverticula which extend anteriorly to form small air-filled bullae near the ear. The significance of this arrangement for sound reception in tarpons is as yet unclear.

The Clupeomorpha

The Clupeomorpha (herringlike fishes) first appear in the Lower Cretaceous. Most of the Recent members (4 families and over 290 species) are primarily marine, although many move easily into brackish and freshwater. They inhabit oceans and seas all the way from the warmest water in the tropics to very cold water in the far north and south. Most are plankton feeders with numerous long gill rakers.

Four specialized character complexes, shared by the Recent Clupeomorpha offer convincing evidence that the group is a genuinely monophyletic assemblage (Grande, 1982a, b has recently provided new information on fossil clupeomorph fishes). The first feature is a specialized connection between the ear and swimbladder. The swimbladder's forward extension divides on each side of the skull to form two large vesicles which are lodged within ossified bullae or expansions of the prootic and pterotic bones (Greenwood *et al.*, 1966; Greenwood, 1973). This type of ear-swimbladder connection is unlike that occurring in any other group of fishes. The second specialization affects the architecture of the neurocranium. Two prominent foramina are found in the temporal (bordered by the frontals and parietals) and the auditory region (surrounded by the prootic, exoccipital, and basiooccipital) (Fig. 25A). The third characteristic feature is the recessus lateralis, a chamber in the pterotic bone into which several of the cranial lateral line canals empty (Greenwood *et al.*, 1966). Finally, extant clupeomorphs have a unique caudal skeleton (Forey, 1975; Gosline, 1960; Greenwood *et al.*, 1966). The urostyle (Fig. 25B) is composed of uroneural one and the terminal vertebral centrum, and hypural one is autogenous—separated by a gap from the urostyle (Fig. 25B: arrow).

The Clupeomorpha and the next major clade to be discussed, the Euteleostei (Fig. 14), appear to be more closely related to each other than either is to any other group of teleosts (Patterson, 1977b; Patterson and Rosen, 1977). In both groups an important innovation is present, increasing the versatility of the feeding apparatus. The upper pharyngeal jaws, which are supported by the first three pharyngobranchials, have a well-anchored armor of teeth formed by the complete fusion of the toothplates to the endochondral pharyngobranchial elements (Nelson, 1969a). Similarly, in the lower pharyngeal jaw the tooth plates fuse to ceratobranchial five. One other significant character uniting the Clupeomorpha and Euteleostei is the co-ossification of the angular and articular bones of the lower jaw (Nelson, 1973). In more primitive groups, the dermal toothplates are only loosely attached to the gill arch elements, and other patterns of lower jaw bone fusion occur. Other features corroborating Clupeocephalan monophyly are summarized in Figure 14.

Clupeomorph relationships have yet to be precisely defined. We provisionally follow Nelson (1970) for most groups, and represent the interrelationships of the clupeoid lineages as an unresolved polychotomy (Fig. 26). The Denticipitoidei contains only the primitive *Denticeps clupeoides* (Clausen, 1959; Greenwood, 1968) from the freshwaters of Nigeria. *Denticeps* bears numerous small denticles on the skull and parts of the body. The Clupeoidei contains the remaining extant clupeomorphs: the Chirocentridae (Wolfherrings; the only predaceous clupeomorphs), Clupeidae (herrings and menhaden), Dussumieriidae (round herrings), Engraulidae (anchovies), and the Pristigasteridae (sometime ranked as a subfamily of the Clupeidae).

Fossil clupeomorphs have been de-

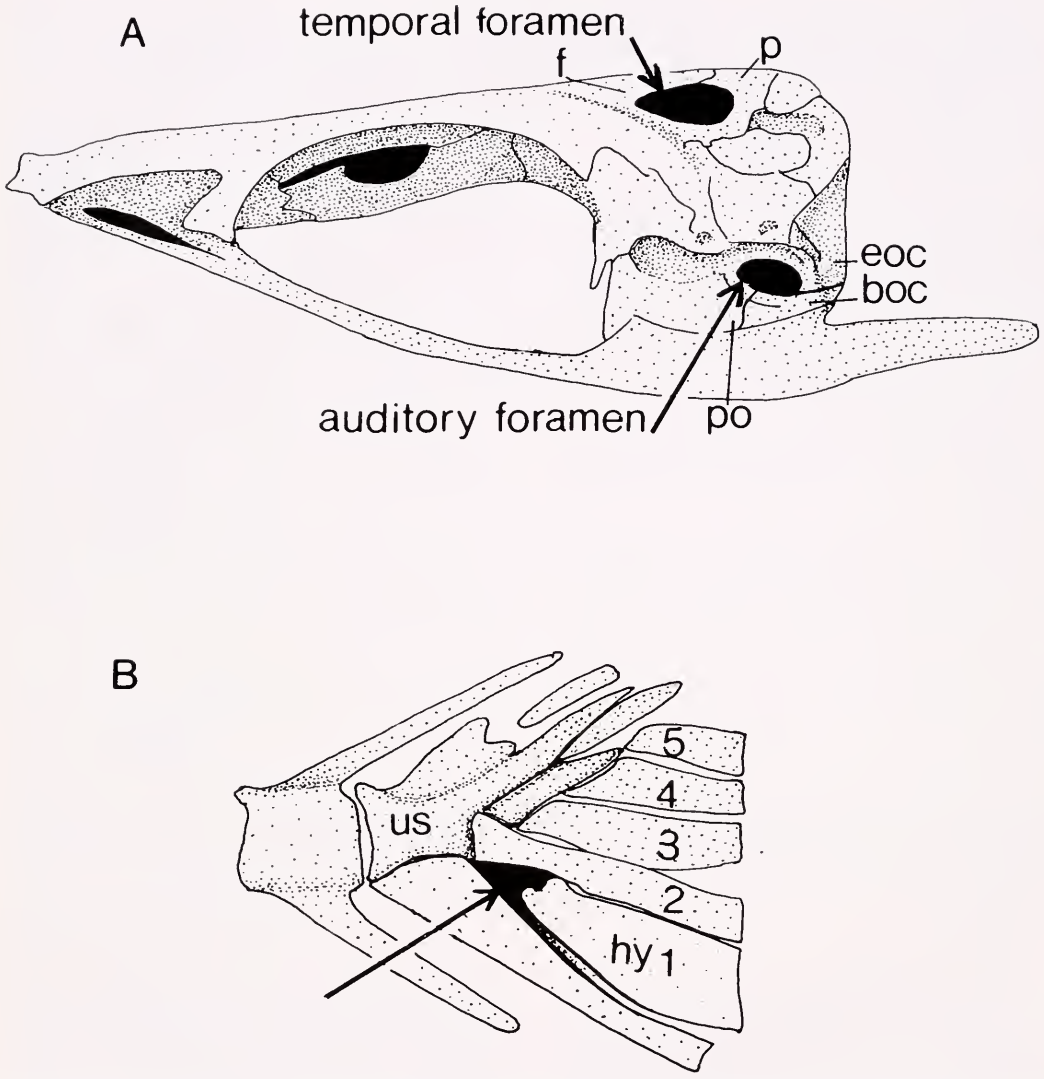


Figure 25. A. Lateral view of a clupeomorph neurocranium, showing the temporal and auditory foramina, surrounded respectively by the frontal (f) and parietal (p) bones, and by the prootic (po), basioccipital (boc) and exoccipital (eoc). B. Lateral view of a clupeomorph caudal skeleton showing the gap between the "urostyle" (us) and the first hypural (hy 1).

scribed by Forey (1973c; 1975), Greenwood (1960), and Patterson (1970), and the relationships of these forms to the Recent Clupeomorpha are summarized in Figure 26.

The major evolutionary trends within the Clupeomorpha are not yet clear due to the lack of a corroborated phylogenetic hypothesis. However, it is evident that there has been a repeated and independent loss of teeth on the jaws and gill arches (Forey, 1975), a reduction and loss of branchiostegal rays, and the development of a long and very complex digestive tract with a "gizzard-like" structure (Nelson and Rothman, 1973). In addition,

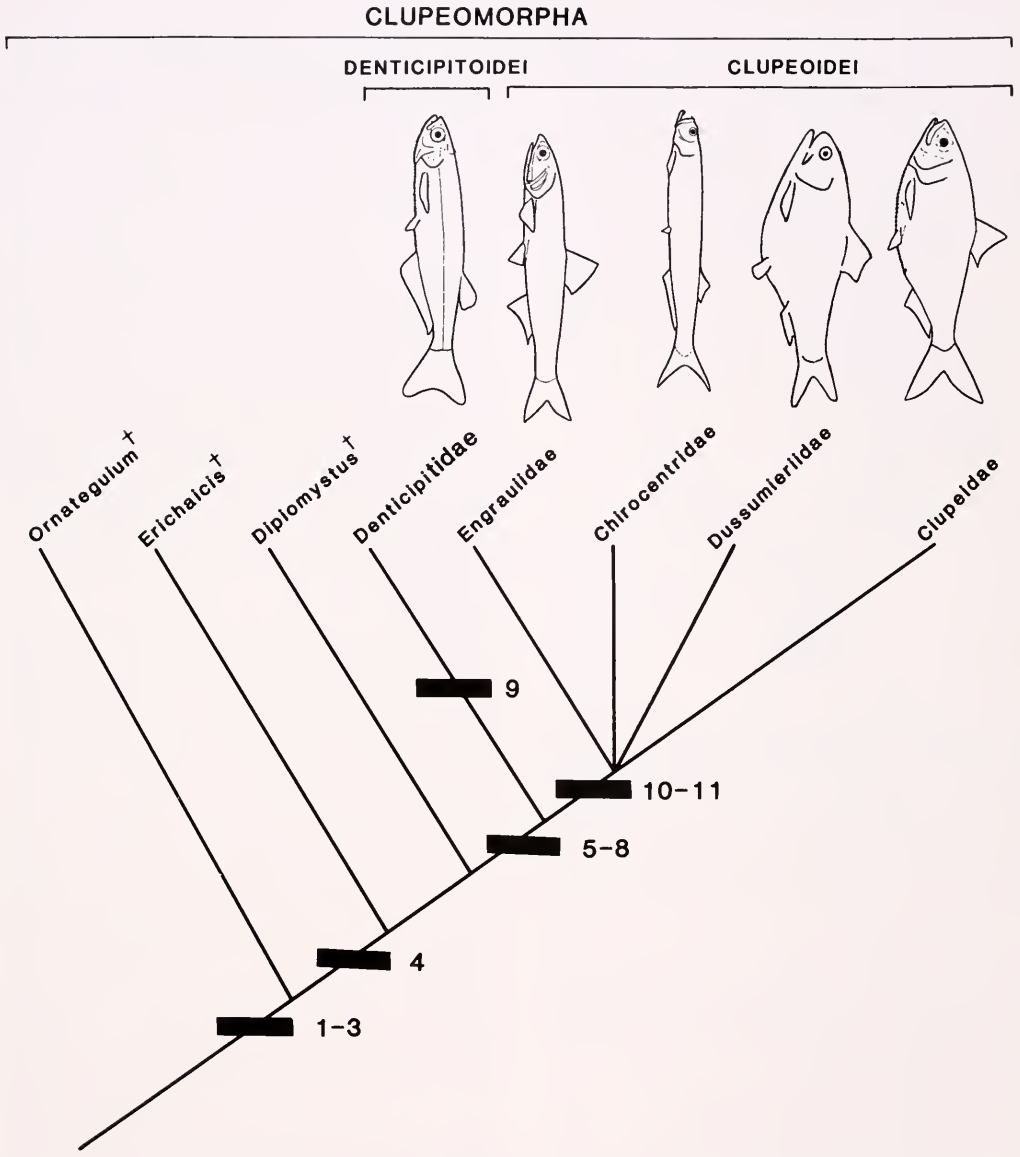


Figure 26. Interrelationships of the major groups of the Clupeomorpha. Three fossil taxa are included. Major specializations characterizing the various lineages are: **1,** autogenous hypural number one; **2,** hypural two fused with ural centrum one (these two characters are also found in several primitive euteleosteans and not in *Erichalcis* (Forey, 1975); **3,** fusion of the median and lateral extrascapulars with the supraoccipital and parietal bones (indicated in part by the presence of a sensory canal in the supraoccipital, Patterson, 1970); **4,** abdominal scutes present; **5,** presence of a recessus lateralis; **6,** temporal foramen present; **7,** post-temporal groove present; **8,** prootic and pterotic bullae present and enclosing an intracranial swimbladder diverticulum (this character is not known in fossil forms although Forey (1975) has suggested that the prootic bulla evolved before the pterotic bulla and may be a unique feature of all clupeomorphs); **9,** denticles on skull bones and some trunk scales (see Greenwood (1968) for additional characters); **10,** third pharyngobranchial bones with long medial processes; **11,** two divisions of the levator arcus palatini muscle (Forey, 1975). The interrelationships of the clupeoids are a matter of dispute and additional families such as the Pristigasteridae and Congothrissidae may be recognized. (Drawings of the fishes adapted from J. S. Nelson [1976], courtesy of John Wiley Publishing Co.)

the clupeoids have evolved an upward extension of the space behind the fourth gill arch bordered anteriorly and posteriorly by the interdigitating edges of specialized gill rakers. The entire organ is called an epibranchial organ (Nelson, 1967a). As the gill arch elements bearing these rakers move toward one another, any small food in the epibranchial organs will be compacted into manageable masses or ground up. These morphological specializations are correlated with the development of mechanisms for the microphagous habits so characteristic of the vast majority of clupeoids.

The Euteleostei

The Euteleostei is an extremely large clade containing a greatly varying array of over 25 orders, 375 families, and 17,000 species. The current definition of the Euteleostei, although it has not been seriously challenged, is "far from satisfactory" (Patterson and Rosen, 1977). Three main characters corroborate euteleostean monophyly, although these are generally shared by primitive euteleosteans and have been lost in the more derived forms (Patterson and Rosen, 1977: 130): 1) the presence of an adipose fin posterior to the dorsal fin, 2) nuptial breeding tubercles on the head and body (Collette, 1977; Wiley and Collette, 1970), and 3) an anterior membraneous component to the first uroneural (Figs. 14, 28). Further evidence corroborating monophyly of this group is highly desirable.

Primitive Euteleostean Fishes

In 1966, Greenwood *et al.* combined into a group, the superorder Protacanthopterygii, a wide variety of fishes which they considered to be basal "Division III" forms (Greenwood *et al.*, 1966: Fig. 1, p. 366). The Protacanthopterygii included the salmoniform, stomiatiform, alepocephaloid, myctophid, neoscopelid, and, questionably, the ostariophysan fishes. Rosen (1973) conducted a critical analysis of the relationships of this assemblage and removed the stomiatiform, neoscopelid, myctophid, ostariophysan and alepocephalid fishes to their current location on the euteleostean cladogram (Fig. 14). These groups will be discussed below. Rosen (1974) then considered the only remaining subgroup, the Salmoniformes, to be monophyletic and coextensive with the Protacanthopterygii. The evidence for monophyly included 1) enlarged toothplates associated with but not fused to the fourth pharyngobranchial and 2) fusion of the third gill arch toothplate to the third pharyngobranchial (Fig. 27). As we have noted above, however (Fig. 14: sp. 129), fusion of toothplates to the endochondral gill arch elements is a clupeocephalan feature, and does not support monophyly of clades within the Euteleostei.

Fink and Weitzman (1982) have dealt the final blow to the concept of a natural Protacanthopterygii, and have shown that the esocoids do not belong in this assemblage, that present data are not sufficient to resolve a dichotomy between the Ostariophysi, Euteleostei, and argentinoids plus osmeroids. The Salmonidae is provisionally considered to be the sister group of the Neoteleostei. Their hypothesis of the relationship of these groups is depicted in Figure 28. Because of the well-corroborated monophyletic nature of the Ostariophysi, we will discuss this group in detail below. Here, under the admittedly inadequate heading "primitive euteleostean fishes," we consider the esocoids, salmonids, osmeroids (*sensu* Fink and Weitzman, 1982), and argentinoids. The phylogenetic relationships of these groups as depicted in Figure 28 should be regarded as highly tentative. Due to the importance of the taxa discussed here both for evolutionary research and for fisheries management and biology, the systematic relationships of these fishes deserve considerable attention. Because of the virtual obliteration of the original Protacanthopterygii, we do

not advocate use of this term, at least until lower euteleostean systematic research provides a well-documented monophyletic group to which the term can be applied.

Esocae. This clade, containing the pikes and pickerels (Esocidae) as well as the mudminnows (Umbridae), may be the most primitive euteleostean clade. Esocids retain the primitive dentigerous toothplates on the fourth basibranchial, lacking in more derived euteleosteans, and this may be evidence of their primitive position relative to other euteleosteans (Fink and Weitzman, 1982). The teeth on the tongue of esocids are small and uniform (Fig. 29), as are the teeth on the basibranchial elements behind the tongue. The adipose fin is absent, but this may be related to the posterior position of the dorsal fin. The maxillae of esocids are toothless, although they do form part of the gape, swinging anteriorly during prey capture as in *Amia* and *Salmo* (Lauder, 1979; Rand and Lauder, 1981). The body form of esocids, with most of the lateral fin area located far posterior to the center of mass, reflects the rapid accelerations used during prey capture and the generally poor cruising performance of these fishes (Webb and Skadsen, 1980). The pikes, pickerels, and mudminnows are restricted to the freshwaters of the northern hemisphere, although *Lepidogalaxias*, considered by Rosen (1974) to be an esocid, (Fink and Weitzman [1982] have questioned this) is a small fish from Western Australia.

Salmonidae. This group includes the trout, salmon (*Salmo* and *Oncorhynchus*), charr (*Salvelinus*), whitefish (*Coregonus*), and the grayling (*Thymallus*). These forms were originally confined to the northern hemisphere before shipment of salmonids to stock southern streams occurred. The small family Galaxiidae is often included with the Salmonidae in the order Salmonoidei, but we follow Fink and Weitzman (1982) in grouping galaxiids with Osmeroidei.

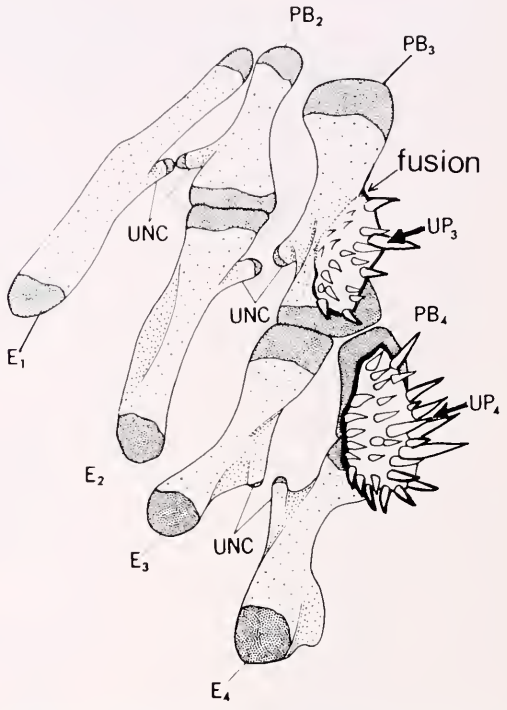


Figure 27. Dorsal gill arch skeleton, right side ventral view, of the "protacanthopterygian" *Novumbra*. Fusion of the toothplate (UP_3) to the third pharyngobranchial (PB_3) is indicated. Other tooth plates (UP_4) are not fused to the gill arch elements. The fourth upper toothplate (UP_4) is the dominant element. (Modified from Rosen, 1974.)

Other abbreviations: E_{1-4}, epibranchials; UNC, uncinate process.

There is relatively little evidence corroborating the monophyly of this group, although Rosen (1974) suggests that the tip of the posterior neural arch of the last caudal vertebra is joined to the first uroneural, and can be used to define osmeroids. Fink and Weitzman discuss two characters which link the salmonids to the Neoteleostei and are suggestive of a sister group relationship (Fig. 28). 1) In salmonids and neoteleosts, both the exoccipital and basioccipital articulate with the anterior vertebrae. In more primitive groups, only the basioccipital is involved in the articulation. 2) Paired cartilage nodules lying anterior to the ethmoid and attached to the premaxillae are suggested

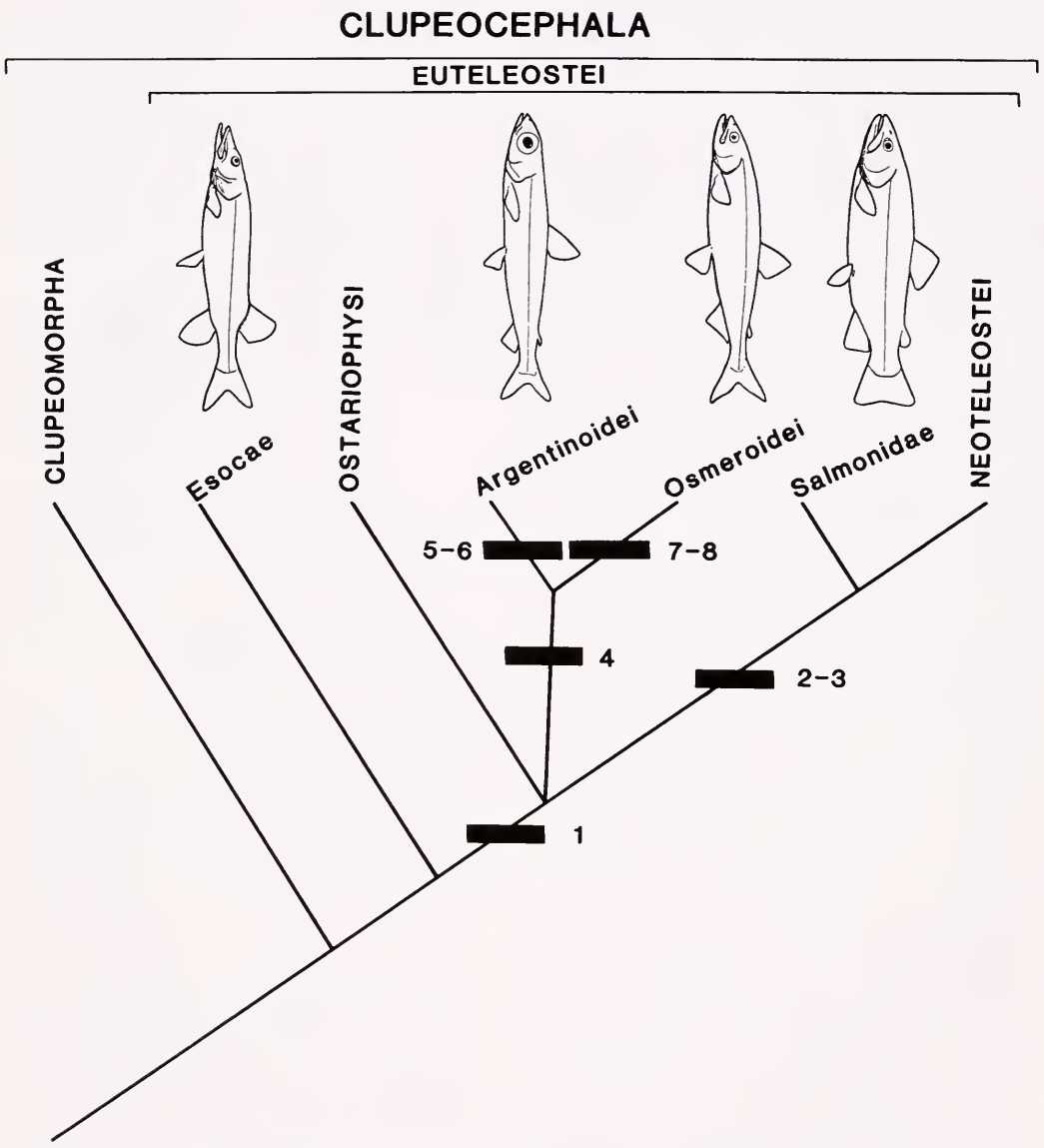


Figure 28. Interrelationships of primitive euteleosteans following the tentative hypothesis suggested by Fink and Weitzman (1982). Specializations characterizing the Clupeocephala, Euteleostei, and Neoteleostei are summarized in Figure 14. The characters are: **1,** loss of the dentigerous toothplate on basibranchial four; **2,** cartilage nodules (homologous to the rostral cartilage of euteleosts) between the ethmoid and premaxillae; **3,** both the basioccipital and exoccipital articulate with the first vertebra; **4,** fusion of the posterior neural arches in the caudal fin with either the uroneural or ural vertebra one, **5,** specialized "tongue-bite" mechanism between basihyal and mesopterygoid teeth (Fink and Weitzman, 1982); **6,** loss of basisphenoid (this bone is also absent in ostariophysans; Fink and Weitzman, 1982); **7,** basibranchials toothless; **8,** "crumenal organ" present and the posterior aspect of the fifth ceratobranchial associated with a complex accessory cartilage (see Greenwood and Rosen, 1971). (Drawings of fishes from J. S. Nelson [1976], courtesy of John Wiley Publishing Co.)

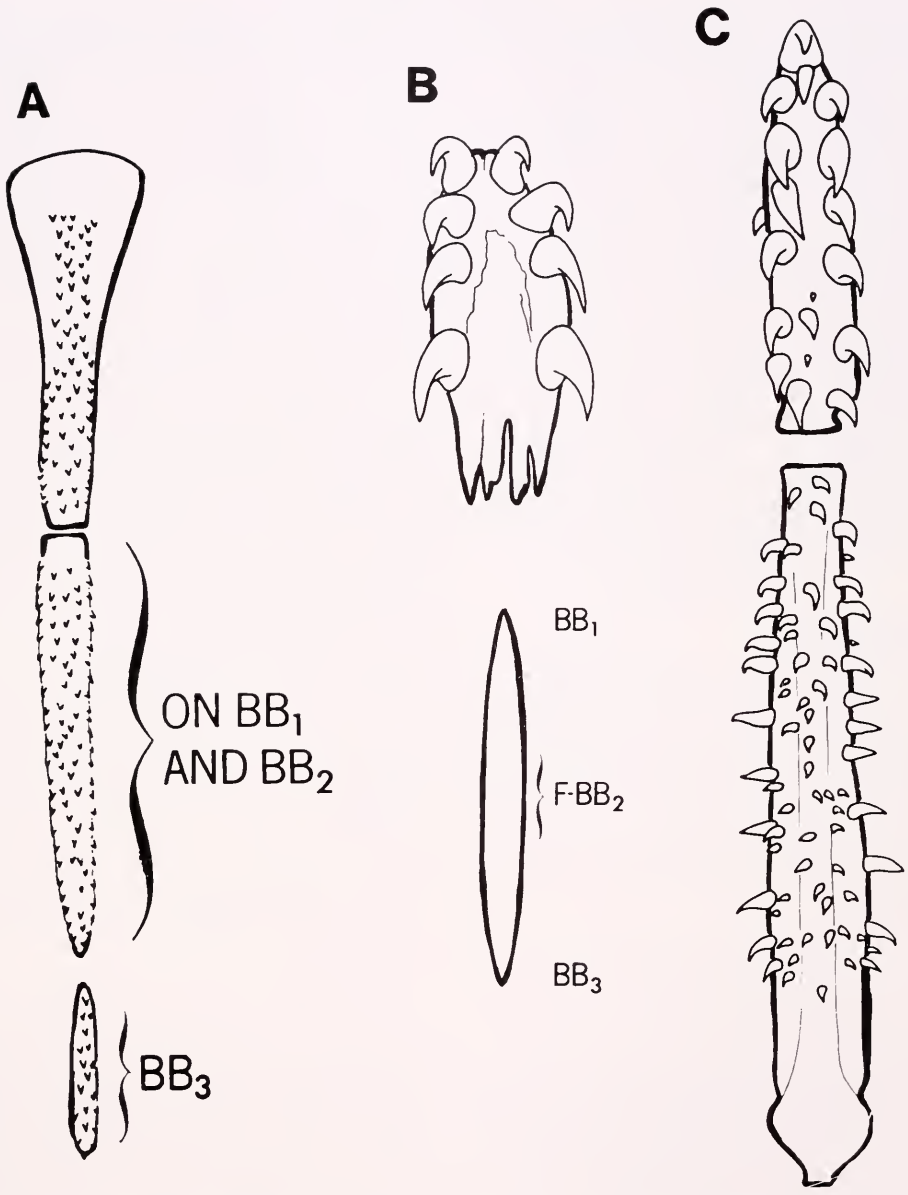


Figure 29. Dorsal view of dermal basihyal and basibranchial elements. A. Esocoids (*Esox*) with uniform and small teeth. B. Salmonoids (*Salvelinus*) showing the terminal pair and pattern of fangs. C. Osmerids (*Retropinna*) with the alternating pattern and terminal fang. (Slightly modified from Rosen, 1974.)

to be homologous with the ethmoid cartilage of the Neoteleostei.

Argentinoids and Osmeroids. The evidence for including the galaxiids within the Osmeroidei is threefold (Fink and Weitzman, 1982). First, both galaxiids and osmeroids lack an orbitosphenoid bone, although the lack of this bone in many

other primitive euteleosteans severely limits the utility of this character. Secondly, both taxa lack a basisphenoid bone. Finally, osmeroids and galaxiids have large fanglike teeth on the basihyal and basibranchial bones (Fig. 29C) which bite (shear) against palatal arch teeth in a similar manner to that described above for osteoglossomorph fishes. Most other primitive euteleosteans lack teeth on the palatoquadrate. Fink and Weitzman (1982) propose a sister group relationship between argentinoids and osmeroids (Fig. 28) on the basis of enlarged marginal basihyal teeth (Fig. 29C), and the occurrence of "platelike" bone on some neural and haemal spines. It should be clear from this discussion that the relationships of these "lower" euteleostean fishes are in need of a comprehensive analysis.

The Ostariophysi

The ostariophysan clade comprises nearly three-quarters of the freshwater fishes of the world and is thus by far the dominant component of this fauna. The 6,000 species included in the Ostariophysi run the gamut from the small South American tetras to the poisonous marine catfishes and the weakly electric gymnotid "eels."

The four major monophyletic groups within the Ostariophysi, the Gonorynchiformes (milkfishes), Characiformes, Cypriniformes (carps and minnows), and Siluriformes (catfishes and gymnotids) are united by many shared characters (Fig. 30). A particularly interesting one is the presence of epidermal "alarm substance cells," a type of club cell (Fig. 30: character 3) which exudes an alarm substance (Pfeiffer, 1974, 1977; first discovered by Karl von Frisch, in 1938) when the cells are damaged. A wounded fish releases alarm substance into the surrounding water, and adjacent fish sense the substance and radically alter their behavior pattern, often scattering immediately in all directions and diving for the bottom—presumably an anti-predation behavior. The fright reaction does not appear to be specific to taxa within the Ostariophysi, and alarm substance extracted from the skin of one group will cause a fright reaction in members of other taxa. The occurrence of fright cells and fright reaction is a shared feature of all ostariophysan fishes and has not yet been confirmed in any other actinopterygian. Another key character (in addition to the occurrence of histologically distinctive breeding tubercles on the body and shared features of caudal anatomy, Fig. 30) is a specialization of the anterior cervical vertebrae and ribs. In the gonorynchiform fishes, the first pleural rib, which articulates with the third vertebra, is expanded and supports a thickened peritoneum that partially invests the anterior chamber of the swimbladder. This condition represents a similar configuration of the swimbladder and pleural ribs to that which is proposed to have occurred in the evolution of the Weberian apparatus characteristic of the remaining ostariophysan fishes (Fig. 30: character 5; Rosen and Greenwood, 1970). Other characters in the anterior vertebrae which characterize all ostariophysans are 1) expanded anterior neural arches which form a roof over the neural canal posterior to the foramen magnum, and 2) loss of the free anterior neural arch (Fink and Fink, 1981).

The Weberian apparatus, named after its discoverer, characterizes the non-gonorynchiform ostariophysans, the Otophysi (Figs. 30, 31). This complex structure consists of five paired bony elements (homologous to neural arches, pleural ribs, and their parapophyses; Rosen and Greenwood, 1970) that form a link between the anterior chamber of the swimbladder and the ear. The five bony elements, the os suspensorium, the tripus, the intercalarium, the scaphium, and the claustrum (Fig. 31), are linked to each other by strong ligaments; the wall of the swimbladder, divided into two separate membranes, the tunica interna and the

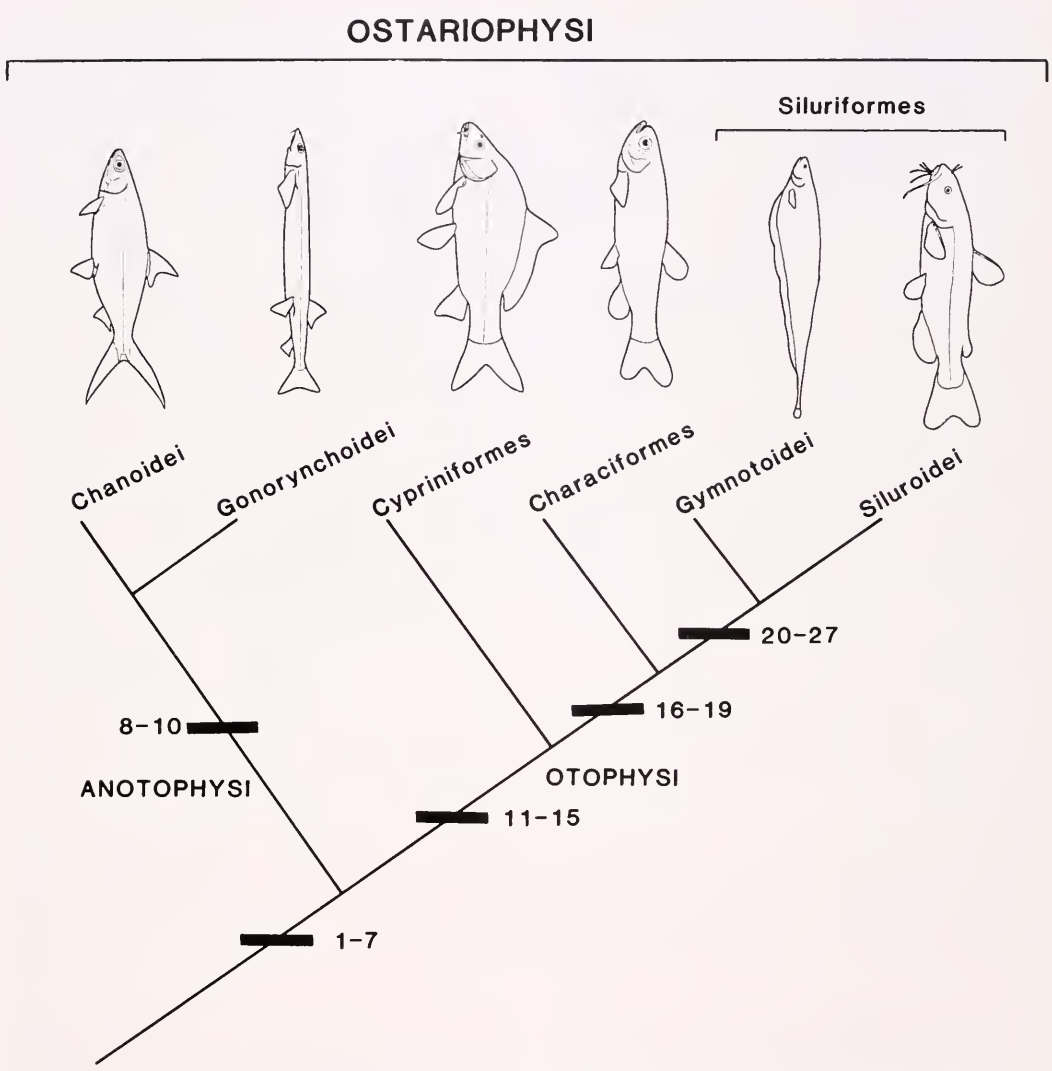


Figure 30. Phylogeny of the ostariophysan fishes (after Fink and Fink, 1981). Only a few of the many characters used by Fink and Fink (1981) to support this cladogram are presented here. The characters are: **1,** loss of dermopalatine; **2,** the swimbladder is divided into a smaller anterior and a larger posterior chamber and the pneumatic duct enters the bladder near the apposition of the two swimbladder chambers; **3,** the presence of fright cells and a fright substance (see text); **4,** swimbladder (anterior chamber) attached to the two anterior pleural ribs; **5,** modification of the anterior cervical vertebrae including loss of the anteriormost supraneural and an enlarged and mobile first pleural rib (see Fink and Fink, 1981); **6,** all anterior haemal spines are fused to the centra; **7,** great reduction in size of the parietal and interorbital septum; **8,** the presence of an epibranchial organ; **9,** absence of teeth on ceratobranchial five; **10,** extensive joint between the exoccipital and neural arch one; **11,** second supraneural is absent; **12,** distinctive specialization of several anterior supraneurals which form a joint with the third and fourth vertebrae; **13,** presence of a Weberian apparatus; **14,** caudal skeleton with a uniquely compound terminal centrum consisting of the last two ural centra, the first preural centrum, and the two anterior uroneurals; **15,** hypural two fused to the compound centrum; **16,** vomer articulates with the mesethmoid anterodorsally; **17,** maxilla positioned posterolateral to the mesethmoid and not articulating with it; **18,** the scaphium extends far anterior to the first vertebral centrum; **19,** Baudelot's ligament attaching to the posterior part of the skull; **20,** intercalar lacking; **21,** scleral bones absent; **22,** supraorbital bone absent; **23,** only one pharyngobranchial toothplate present; **24,** absence of articular process of the intercalarium; **25,** distally bifurcate Baudelot's ligament; **26,** posterior pectoral fin rays offset from the anteriormost ray; **27,** medial ossification of the dorsal and anal fin radials is absent. (Drawings of fishes from J. S. Nelson [1976], courtesy of John Wiley Publishing Co.)

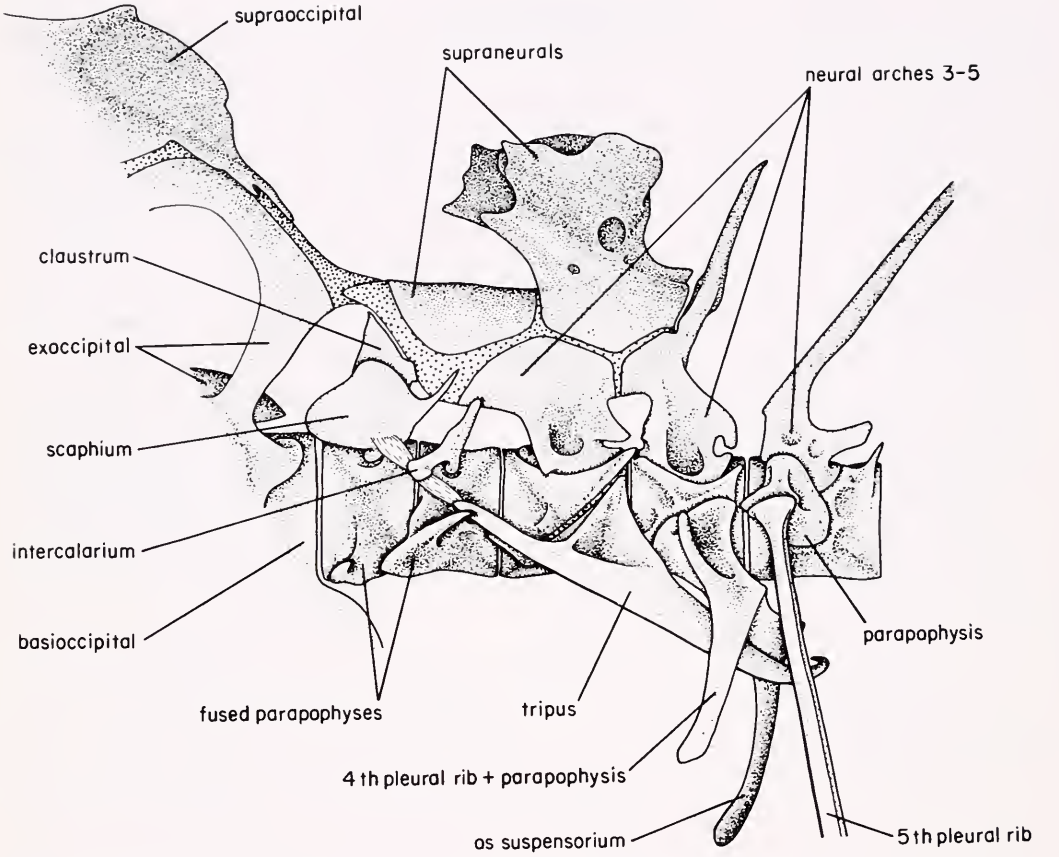


Figure 31. Lateral view of the Weberian apparatus in characiphysans. Anterior is to the left. (From Fink and Fink [1981], reprinted by permission of the Council of the Linnean Society of London.)

tunica externa, attaches to the os suspensorium and the tripus. Differential movement of these two membranes when sound waves impinge on the swimbladder causes oscillations in the chain of Weberian ossicles that are transmitted to the ear (Alexander, 1966a, 1975).

The ear and otic region of the skull are also highly modified in ostariophysan fishes in connection with the Weberian apparatus. The saccular and lagenar otoliths are located far posteriorly in the cranium, and a connection has developed between the two paired sacculi with a median posterior extension, the sinus impar. It is onto the wall of the endolymph-filled sinus impar that ligaments from the scaphium attach, and this connection allows the transmission of sound into the inner ear. There is increasing evidence that this complex otophysic connection actually does result in a substantially improved hearing ability, especially at the higher frequencies (Popper and Coombs, 1982; Popper and Fay, 1973; Tavolga, 1976).

Until very recently, most hypotheses of the relationship of the major ostariophysan subgroups were based on concepts of ancestry and descent: many groups had specializations that prohibited them from being ancestral to other taxa. The publication of a major new synthetic analysis of ostariophysan relationships (Fink and

Fink, 1981) has focused on character distributions and has resulted in a detailed and highly corroborated hypothesis of relationship. This hypothesis is presented in Figure 30 with a portion of the extensive evidence supporting it. The Ostariophysi is separated into two lineages, the Anotophysi containing the order Gonorynchiformes and the Otophysi. The Otophysi in turn is divided into two monophyletic taxa, the Characiphysi with the orders Siluriformes and Characiformes (tetras, pacus, piranhas), and the Cypriniphysi (minnows, suckers, hill-stream fishes, carps, and loaches).The Siluriformes are in turn divided into two suborders, the Siluroidei (catfishes) and the Gymnotoidei (electric gymnotid fishes). This scheme of relationships differs significantly from past attempts to decipher ostariophysan phylogeny, especially in placing catfishes and gymnotids as sister groups (Fig. 30).

Gonorynchiform Fishes. The Order Gonorynchiformes contains four families, three with only one species and one with about twelve. Milkfish (Chanidae) are mostly marine and brackish water fishes found in southeast Asia where they are extremely important as a food fish, often reaching well over a meter in length. Two other families of gonorynchiforms, the Kneriidae and Phractolaemidae, have protrusible upper jaws and are found in the freshwaters of tropical Africa. The Family Gonorynchidae contains only one species and together with the Kneriidae and Phractolaemidae forms the Suborder Gonorynchoidei. *Gonorynchus* is found in Indo-Pacific marine habitats and has a very elongate body shape, and a protrusible jaw. It apparently feeds on small bottom-dwelling invertebrates, and its biology is poorly known. The gonorynchiforms are a well-corroborated monophyletic group (Fig. 30), and Fink and Fink (1981) have suggested that *Chanos* is the primitive sister group of all other gonorynchiforms.

Characiformes. The characiforms, together with the cypriniforms (minnows) and siluroids (catfishes), comprise the bulk of the world's freshwater fauna. It is somewhat surprising given the importance of these groups and over a century of research that their interrelationships are not better known. One reason for the past difficulty in deciphering the interrelations of many ostariophysan fishes is the tremendous morphological and ecological diversity of each subgroup. The characiforms, for example, with over 1,000 living species (and maybe a quarter that number still undiscovered) have radiated extensively in South America and to a lesser extent in Africa and Central America. In the Amazon River basin, one of the most ichthyologically diverse areas in the world, over 43 percent of the fishes are characiforms (Roberts, 1972). The Ostariophysi as a whole compose 85 percent of the Amazon fish fauna and 54 percent of the Congo fishes (Roberts, 1972). Reductive evolution and neoteny have also been common in characiform fishes (Weitzman, 1962) and have compounded the difficulties of working with such a vast species assemblage. Characiforms have been divided (somewhat arbitrarily) into sixteen families (Greenwood *et al.*, 1966) of which four are African. The family Hepsetidae contains only *Hepsetus odoe*, an elongate piscivorous and insectivorous pikelike fish, which is widely distributed in Africa and represents a relatively generalized morphology. The families Citharinidae and Distichodontidae (Vari, 1979) contain deep-bodied African fishes while the Ichthyboridae, also African in distribution, contains about nine genera of elongate fishes, many of which are reported to eat the fins and scales of other fishes. The remaining African taxa are usually grouped in the family Characidae, the best known African forms being *Alestes*, an omnivorous widely distributed genus, and *Hydrocynus*, a predator reaching over a meter in length. The remaining members of the Characidae are found in Central and South America and are enormously diverse, the family being divided into a

number of subfamilies. The American Characidae includes the piranhas (*Serrasalmus*), the glandulocaudine fishes which have specialized "caudal glands" on the caudal fin, the tetragonopterine characids, best known for the small colorful tetras but also including the generalized *Astyanax*, and the bryconine fishes (*Brycon*) and *Chalceus*. Other South American characiform families range from the family Erythrinidae (Roberts, 1969), with three genera of predaceous fishes, to the specialized Cynodontidae (Howes, 1976) and Gasteropelecidae—the freshwater hatchetfishes which are capable of making short (10 m) flights just above the surface of the water with their greatly enlarged pectoral fins. The family Ctenoluciidae, the pike-characins, are elongate piscivorous fishes, while the Prochilodontidae, Curimatidae, and anostomidae are deeper bodied and eat mud, detritus, and insects.

Many characiforms show complex patterns of tooth morphology and replacement (Roberts, 1967), and their extensive radiation has resulted in a wide range of trophic specializations ranging from mud and detritus feeders to the specialized scale eating forms (Roberts, 1970). The trophic interactions between fishes in the world's tropical freshwaters have been recently reviewed in Lowe-McConnell (1975); also see Fink and Fink, 1979). Evidence for characiform monophyly is summarized in Figure 30.

Cypriniform Fishes. The primitive sister group of the characiphysi is the Cypriniformes (Fig. 30) which is a clearly monophyletic group based on characters such as the kinethmoid bone and the unique upper jaw mechanism (Alexander, 1966b), the dorsomedial palatal process, and the structure of the premaxilla and pharyngeal jaw complex (see Fink and Fink, 1981). Cypriniforms are usually divided into six families, one of which, the Cyprinidae, contains the vast majority (80%) of all cypriniform fishes. Cypriniforms lack (except in a few species) the primitive euteleostean adipose fin (Fig. 14: character 11; see Fig. 30 for the presence of the small adipose fin, located posterior to the dorsal fin, in most characiform groups) and lack teeth on their oral jaws which are protrusible. The protrusible cypriniform jaw evolved independently from the acanthopterygian protrusible jaw discussed below. The cypriniform radiation is one of the few among the actinopterygian fishes that contains a large proportion of herbivores and very few piscivorous taxa are known (Howes, 1978). Correlated with extraction of nutrients from thick-walled algal cells, the two families containing the largest proportion of herbivores, the Cyprinidae and Catostomidae, possess strong grinding and crushing pharyngeal jaws. Primitively, teleostean pharyngeal jaws are of relatively limited mobility, being used primarily to aid the manipulation of prey in the buccopharyngeal cavity prior to deglutition. In cyprinids and catostomids, however, the lower pharyngeal jaws are hypertrophied and form massive bony elements which can be apposed to a horny pad located on the basioccipital bone (Eastman, 1971, 1977). Thus, the pharyngeal jaws in these cypriniforms "chew" against the base of the skull and are capable of strong grinding motions (Sibbing, 1982). The diversity in tooth structure on the lower pharyngeal jaws correlates with the diversity in feeding habits.

The speciose family Cyprinidae is widely distributed in the freshwaters of North America, Africa, Europe, and Asia; it is completely absent from South America. All Cyprinidae lack a true stomach and have an elongate intestine, a condition that would seem to correlate with a diet containing a high proportion of indigestible material (Kapoor *et al.*, 1975). The North American cyprinid fauna contains only about 200 species, much greater cyprinid diversity occurring in Africa and Eurasia and including the well-

known carp (*Cyprinus*) and goldfish (*Carassius auratus*). The family Catostomidae, suckers, has a highly disjunct distribution and occurs in North America and China. Suckers have large fleshy lips and are remarkable for the large number of hybrid populations which occur between species of the family. The remaining families of cypriniforms are small elongate forms with a subterminal mouth and inhabit the freshwaters of Eurasia and Africa. The Gyrinocheilidae (suckerbelly loaches), Psilorhychidae, and Homalopteridae (hillstream loaches) all inhabit freshwater streams and use suctorial mouths or modified pelvic fins as an aid in adhering to the substrate in fast-moving waters. The family Cobitidae (loaches) are elongate bottom dwellers occurring with greatest diversity in Southeast Asia but also with a very restricted African distribution.

Siluroid Fishes. The catfishes form a diverse group (about 2,000 species in 31 families) of highly modified fishes which have a distinctive morphology (Fig. 30). Characteristics of this group include large spiny first rays of the pectoral and dorsal fins which may be locked in the erect position, the absence of true scales—the body is naked or has thick bony plates, and from one to four pairs of barbels which presumably serve tactile and gustatory functions. Other specializations are the loss of a number of skull bones, characteristic modifications of the Weberian apparatus (Alexander, 1964), and a distinctive pectoral girdle modified to support and form the locking mechanism for the pectoral fin spines (Fig. 30; Fink and Fink, 1981). In many groups, a unique mechanism for moving the maxillary barbels occurs. This involves modifications of the palatoquadrate and jaw adductor musculature (Gosline, 1976) as well as the reduction of the maxillary bone to a toothless nubbin supporting the barbel.

The most primitive family of catfishes, the relic Diplomystidae of South America, are the only catfish family to retain a toothed maxillary bone. With the exception of this one family, however, the phylogenetic position of the other catfish families is uncertain and further work is badly needed on the interrelationships of the catfishes. Three families are partially or completely marine in habit: the Ariidae and Plotosidae are mainly salt water groups with the latter capable of inflicting painful wounds with their venomous dorsal spine, while the Aspredinidae occupy mostly freshwaters in tropical South America, but some species are brackish or marine in occurrence.

Of the 31 currently recognized catfish families, 13 are endemic to South America (Roberts, 1972). The most speciose families are the Pimelodidae (with about 285 species), the armored Callichthyidae and Loricariidae, together with about 550 species, and the parasitic Trichomycteridae, some of which live on blood obtained through the gills and skin of other fishes. Some species of the genus *Vandellia* may enter the human urethra causing considerable pain. Among the African families, one of the more unusual is the family Malapteruridae, the electric catfishes. These thick-bodied fishes are capable of delivering a strong electric shock. Other families include the air breathing Clariidae, of which one Asian species, the "walking catfish," has been introduced to American waters; the Mochokidae, several species of which normally swim with the ventral side uppermost; and the Amblycipitidae and Amphiliidae that inhabit fast-moving streams. The native European catfish family is the Siluridae, although the introduced ictalurids are now more common; one silurid species reportedly can attain a length of over three meters (J. Nelson, 1976). In North America, the Ictaluridae (bullheads) are the only group of catfishes and are widely distributed throughout the continent.

The feeding habits of catfishes encompass the range from pure herbivory to car-

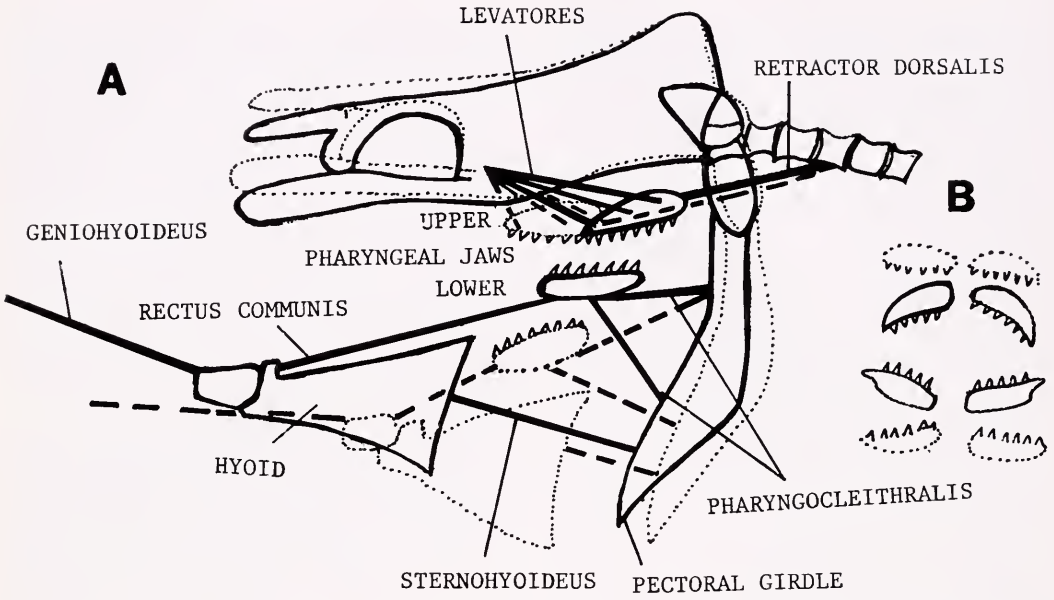


Figure 32. A. Simplified diagram depicting the retractor dorsalis (or retractor arcuum branchialium, RAB) muscle in euteleosts. Solid lines show position and condition of muscles during retraction of the pharyngeal jaws. Bony elements in dotted lines represent positions during protraction. B. Front view of upper and lower pharyngeal jaws during retraction (solid lines) and protraction (dotted line). (After Liem, 1977 *in* A. Kluge (ed.), "Chordate Structure and Function," courtesy of Macmillan Publishing Co.)

nivorous forms, and locomotor habit may vary from the bottom-dwelling loricariids with suctorial mouths to the fast-moving streamlined cetopsid catfishes of South America.

Gymnotoidei. The gymnotoid fishes, a group of special interest to neurobiologists and students of animal behavior because of their electrogenic ability, share a common ancestor with the catfishes (Fig. 30). Characters shared by these two taxa include the structure of the mesethmoid, absence of scleral bones, a greatly reduced ectopterygoid, a single pharyngobranchial toothplate, and electroreceptive capability (Fink and Fink, 1981). The gymnotoids, grouped into four families, are mostly nocturnal and insectivorous, and are remarkable for their ability to generate and detect weak electric signals which are used in navigation and for intraspecific communication. Recent articles on gymnotoid electroreception include Hopkins (1976), Hopkins and Heiligenberg (1978), and Heiligenberg (1977). The family Apteronotidae is the most diverse family of gymnotoids with about ten genera, although gymnotoid systematics at the genus and species level is in need of much further study. Apteronotids are unique among gymnotoids in having neurally derived electric organs which fire at higher frequencies (1000-1800 Hz) than the myogenic organs of the other wave-generating families. The Electrophoridae contains only one species, *Electrophorus electricus*, the electric eel, which can produce a powerful electric discharge and may reach 2.3 meters in length. *Electrophorus* is piscivorous. Gymnotids (Gymnotidae), with about three species, and the Rhamphichthyidae are more elongate than apteronotids and lack a caudal fin. Wave-mode firing of electric organs appears to have evolved at least twice in the gymnotoid

fishes. The gymnotoid fishes are restricted to South and Central America.

The Neoteleostei: The Emergence of a Pharyngeal Retractor Muscle

One of the most striking innovations during the evolution of the Euteleostei is the appearance and differentiation of a unique muscle associated with the upper pharyngeal jaws. This bilaterally paired muscle is known as the retractor arcus branchialium (RAB, Rosen, 1973) or retractor dorsalis (RD, Winterbottom, 1974a). The anterior end of each retractor dorsalis inserts on the dorsal gill-arch elements (pharyngobranchials), and the posterior end may originate from any of the first to sixteenth vertebrae (Fig. 32). Fishes with an RD are grouped together in the Neoteleostei (Fig. 14). Experimental studies (Lauder, 1983; Liem, 1970, 1978) have shown that the retractor muscles play a key role in the manipulation, trituration, and swallowing of prey. In primitive euteleosteans such as *Esox* that lack the retractor dorsalis, protraction and retraction of the upper pharyngeal jaws occurs by alternate activity in the levatores externi one and two which produce posterior movement, and the levatores externi three and four causing protraction (Lauder, 1983). In neoteleosteans the retractor dorsalis forms the retractive component of the upper pharyngeal jaw complex.

Based on both phylogenetic and ontogenetic evidence (summarized in Rosen, 1973; also see Winterbottom, 1974a), the RD's originated from the dorsal, inner striated, longitudinal muscle fibers of the esophagus. Thus the evolution of RD control of the upper pharyngeal jaw had to be preceded by the development of a substantial longitudinal muscle layer at the beginning of the esophagus. The evolutionary history of the neoteleosteans is closely related to changes and specializations of the RD. In this summary, the basic premise is that the Neoteleostei represents a monophyletic assemblage characterized by the specialized upper pharyngeal jaw (among other features), which have a unique functional design with the appearance of an RD (Fig. 14). The following subchapters will trace the evolution of the major groups of the Neoteleostei, starting with the Stomiiformes and Aulopiformes and proceeding to the more advanced Myctophiformes, Paracanthopterygii, and Acanthopterygii.

Characters corroborating the hypothesis of neoteleostean relationships presented here (essentially that of Rosen, 1973) are summarized in Figure 14. Rosen's (1973) hypothesis has been examined and tested by Fink and Weitzman (1982) and Lauder (1983). Several conclusions have emerged from these recent analyses that have special importance for neoteleostean relationships and evolution. 1) The protractor pectoralis muscle, formerly believed to separate the Stomiiformes (which lack this muscle) from all other neoteleosteans (Rosen, 1973; Winterbottom, 1974a) appears to be a primitive gnathostome feature of very scattered distribution within teleosts (Greenwood and Lauder, 1981). It thus does not serve to define a monophyletic taxon within the Neoteleostei. 2) The "A1" division of the adductor mandibulae appears to have evolved independently in at least three lineages of neoteleosteans and is not indicative of neoteleostean monophyly (Fink and Weitzman, 1982). A muscle, termed the A1β, that arises medially on the palatoquadrate and inserts on the maxilla, occurs in stomiiforms, some acanthopterygians, some paracanthopterygians, and some aulopiforms, but not in atheriniforms or neoscopelids. 3) The presence of a median rostral cartilage between the premaxillae and the neurocranium characterizes the Neoteleostei (Fink and Weitzman, 1982). Finally 4), at a higher cladistic level, the occurrence of apharyngohyoideus muscle, with an origin on

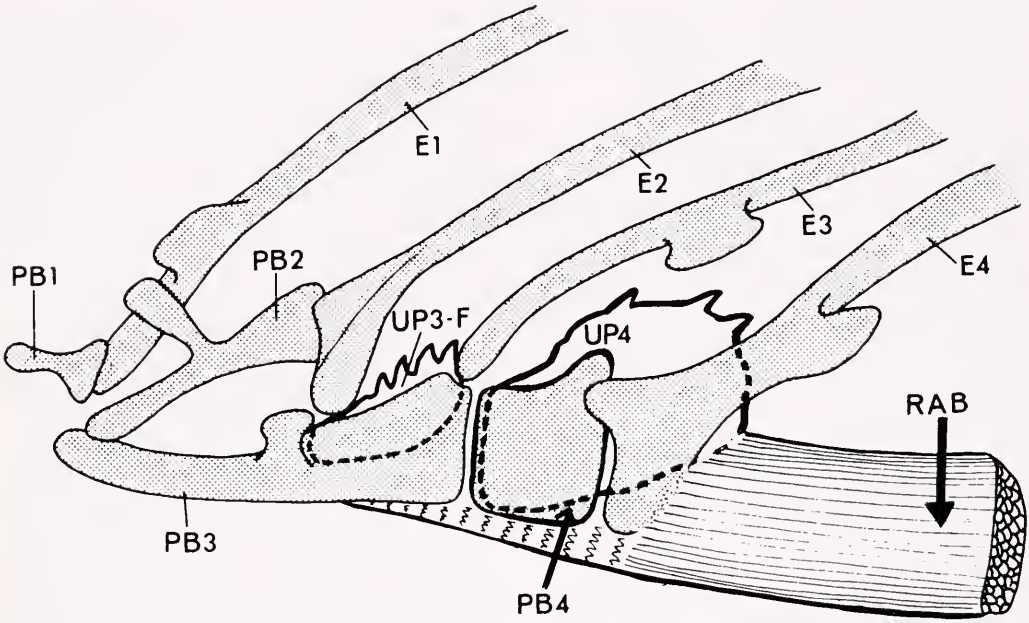


Figure 33. Dorsal gill arch elements and the retractor dorsalis (RAB) muscle in the stomiiform *Astronesthes* (dorsal view). The major muscle insertion is on the dominant fourth upper tooth plate (UP4) and fourth pharyngobranchial (PB4). (Modified from Rosen, 1973.)

Other Abbreviations: E 1–4, epibranchials; PB 1–4, pharyngobranchials; UP, upper pharyngeal tooth plate; UP3-F, upper pharyngeal tooth plate fused to endoskeleton.

ceratobranchial five and insertion on the urohyal, is a characteristic feature of the ctenosquamate fishes (= myctophiforms, paracanthopterygians, and acanthopterygians; Lauder 1982a). Stiassny (in preparation) has found a muscle apparently homologous to the ctenosquamate pharyngohyoideus in several aulopiforms. It is not yet clear if the aulopiforms are nonmonophyletic or if this muscle has been independently acquired in a few aulopiform taxa. The pharyngohyoideus is homologous to the rectus communis muscle of lower teleosts which inserts on hypobranchial 3. The change in insertion to the urohyal marks an important functional shift, because the pharyngohyoideus is then no longer an intrinsic gill arch muscle, and forms the anterior element controlling anteroposterior and lateral movement of the lower pharyngeal jaw. Thus, the Ctenosquamata (Rosen, 1973) possess two functionally important pharyngeal jaw innovations allowing greatly increased control of prey transport and preparation in the pharynx (Lauder, 1983). Other characters relevant to neoteleostean relationships are summarized in Figure 14.

The Stomiiformes

Although stomiiformes are considered to be the most primitive neoteleosteans, the condition of the retractor dorsalis muscle appears to be specialized from the probable primitive condition. The stomiiform upper pharyngeal jaw apparatus has the uncinate process of the second epibranchial obliterated by the development of a direct and broad articulation with the third pharyngobranchial, and the stomiiform RD insertion on the upper pharyngeal jaw is confined to the most posterior toothplate, which is associated with the 4th pharyngobranchial (Fig. 33).

As a result the alignment of the RD is longitudinal. It seems likely that the retractor dorsalis can produce greater excursions in a longitudinal direction than tilting or rocking (dorsoventral) movements of the upper pharyngeal jaws.

Stomiiforms are composed of over eight families, including Gonostomatidae (light fishes), Sternoptychidae (marine hatchet fishes; Weitzman, 1974), Chauliodontidae (viperfishes; Tchernavin, 1953), Stomiatidae (dragonfishes), and some 300 species that inhabit the middle depths of the Atlantic, Indian, and Pacific oceans. They are small, possess photopores, and have a mouth that extends posteroventrally past the eye.

Fink and Weitzman (1982) have discussed characters that establish monophyly of the Stomiiformes. These include: 1) a unique photopore histology, 2) type 3 tooth attachment (Fink, 1981), 3) morphology of the adductor mandibulae muscle, and 4) some branchiostegal rays articulating with the ventral hypohyals.

The Aulopiformes

This relatively small order of worldwide marine fishes embraces two distinct groups: 1) the Aulopoidei, which contains the thread-sail fishes (Aulopidae), greeneyes (Chlorophthalmidae), Bathysauridae, Scopelosauridae, Bathypteroidae and the large-eyed but lens-less Ipnopidae, and 2) the Alepisauroidei, which contains the Synodontidae (lizard fishes), Harpadontidae (Bombay ducks), Alepisauridae, Scopelarchidae, and Evermannellidae (Johnson, 1974).

All aulopiform fishes share a highly specialized feature in the dorsal elements of the second and third gill arches. The second pharyngobranchial is greatly elongated posterolaterally so that its long axis is directed away from the third pharyngobranchial. As a result a gap is present between the second epibranchial and the third pharyngobranchial. This gap is bridged by an uncinate process of the second epibranchial (Rosen, 1973; Fig. 34). It is possible that this bridge offers additional structural strength to the upper pharyngeal jaw apparatus and that it has developed as a response to the new mechanical loading by the retractor dorsalis muscle.

The most generalized condition of the retractor dorsalis muscle (RD) is found in the aulopiforms. The RDs are still surrounded by the outer circular musculature of the esophagus. Anteriorly the RDs fan out to form a flat sheet of muscle that inserts on the fourth epibranchial and the ventromedial edge of the third pharyngobranchial (Fig. 34). Aulopiforms have a protractor pectoralis muscle which originates from the pterotic and inserts on the anterodorsal surface of the cleithrum.

Alepisauroids differ from aulopoids in having longer pharyngobranchials, the loss of the second and fifth upper pharyngeal toothplates, and the development of a very long jaw with an oblique suspension. There is myological evidence that the aulopoids represent the more primitive and generalized forms among the aulopiforms (Rosen, 1973).

The Myctophiformes

This large group of pelagic marine fishes has been abundant and diverse since the Upper Cretaceous and contains the families the Myctophidae (the lanternfishes), with their photophores arranged along the side of the body like portholes, the Neoscopelidae, Evermannellidae (sabertooth fishes, Johnson, 1982) and the Scopelarchidae (the pearl fishes, Johnson, 1974).

The Myctophiformes are thought to be monophyletic since in all species the toothed third pharyngobranchial is the largest toothed element of the upper pharyngeal jaw. The fourth tooth-plate is only half the size of the third and is movably hinged to the third tooth plate. Consistent with these size relations of the toothplates in myctophiforms is the reduction in size of the fourth pharyngobranchial

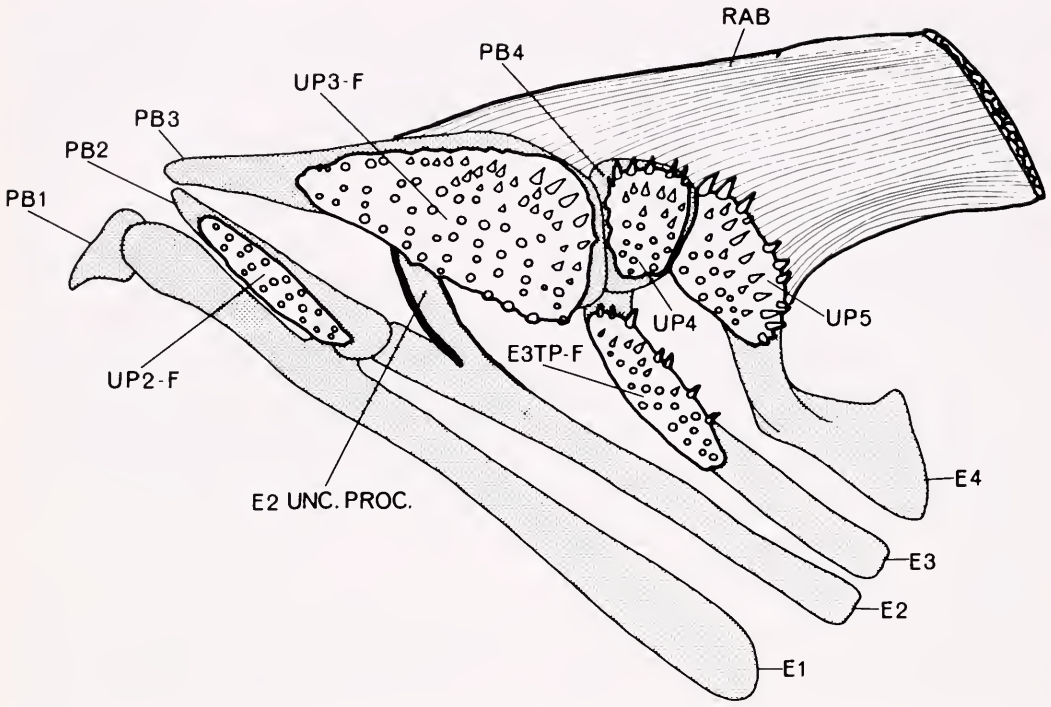


Figure 34. Dorsal gill arch elements and the retractor dorsalis (RAB) muscle in the aulopiform *Aulopus* (ventral view). The muscle fans out to insert on the third and fourth pharyngobranchials and fourth epibranchial. The second epibranchial (E_2) has a prominent uncinate process (E_2UNC. PROC.). (Modified from Rosen, 1973.)

Other Abbreviations: E_{1-4}, epibranchials; PB_{1-4}, pharyngobranchials; RAB, retractor arcuum branchialium or retractor dorsalis muscle; TP, toothplate; TP-F, toothplate fused with endoskeleton; UP, upper pharyngeal toothplate.

and the division of the retractor dorsalis muscle into distinct medial and lateral components or heads (Rosen, 1973). The smaller medial head inserts on the third pharyngobranchial, whereas the lateral component retains the original or primitive insertion on the fourth pharyngobranchial and its tooth-plate (Fig. 35). The appearance of the medial head of the retractor dorsalis inserting exclusively on the third pharyngobranchial indicates that the myctophiforms are aligned with the paracanthopterygians and acanthopterygians rather than with the Aulopiformes (Rosen, 1973). The dual insertions of the retractor dorsalis on the third and fourth pharyngobranchials in myctophiforms furnish the basic system from which the more specialized upper pharyngeal jaws of the paracanthopterygians and acanthopterygians were derived. In myctophiforms we can see the beginning of the trend towards an increasing emphasis on the third pharyngobranchial as the dominant tooth-bearing element in the upper pharyngeal jaw in advanced euteleosteans. Concomitantly in some Acanthomorpha there is a shift of the insertion of the retractor dorsalis from the fourth, or third and fourth, to an exclusive insertion on the third pharyngobranchial.

The Myctophidae (lantern fishes) comprise about 32 genera and about 220 species (Paxton, 1972; Nafpaktitis, 1978; Nafpaktitis *et al.*, 1977). They occur in all oceans from the Arctic to the Antarctic and are known for their daily vertical migrations. At night they migrate to the sur-

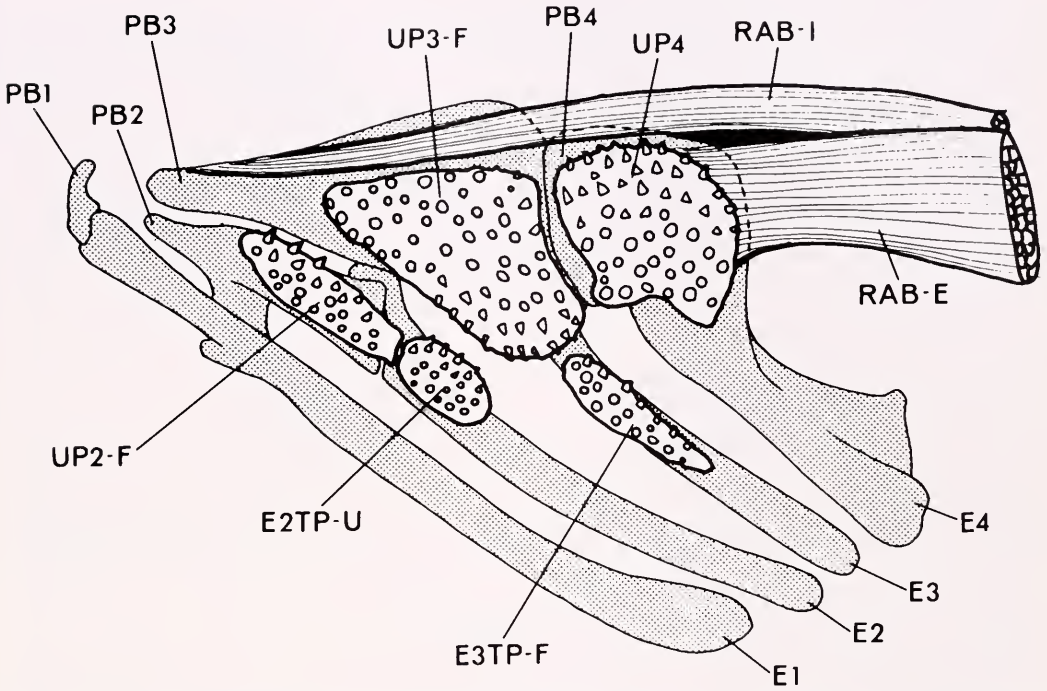


Figure 35. Dorsal gill arch elements and the retractor dorsalis (RAB) muscle in the myctophiform *Neoscopelus* (ventral view). The muscle is subdivided into an internal (RAB-I) and external (RAB-E) division, inserting respectively on the third pharyngobranchial (PB_3) and the fourth upper toothplate (UP_4). (Modified from Rosen, 1973.)

Other Abbreviations: E_{1-4}, epibranchials; PB_{1-4}, pharyngobranchials; RAB-E, external division of retractor dorsalis; RAB-I, internal division of retractor dorsalis; TP-F, toothplate fused to endoskeleton; UP, upper pharyngeal toothplate.

face to feed; with the approach of day they start their return trip into the depths as far as 500 meters. Of course, myctophids are well known for the possession of small photophores arranged in groups and rows on head and body. Because lanternfishes make up a considerable biomass and are able to convert plankton to food for organisms higher on the food chain, they occupy an important position in the trophic ecology of the ocean.

The Neoscopelidae is a small family containing five species (Nafpaktitis, 1977).

The Paracanthopterygii

The concept of the Paracanthopterygii as a monophyletic assemblage has been plagued with problems, ambiguity, and confusion ever since its inception (Rosen and Patterson, 1969). The major difficulty is the lack of a shared derived feature characterizing all paracanthopterygians (Rosen, 1973). Here we offer a provisional scheme of paracanthopterygian relationships, realizing that we may be including unrelated groups.

We include the Percopsiformes (trout-perches), Gadiformes, Batrachoidiformes (toadfishes), Lophiiformes (anglerfishes), and Gobiesociformes (clingfishes), groups representing over 200 genera. The Percopsiformes is known from the Cretaceous, whereas the other four orders date from the Eocene. Paracanthopterygians are predominantly marine fishes. Only five genera of the percopsiforms, the gadiform *Lota*, a few brotulids, some batrachoidiforms and the fluviatile gobiesocids are freshwater fishes.

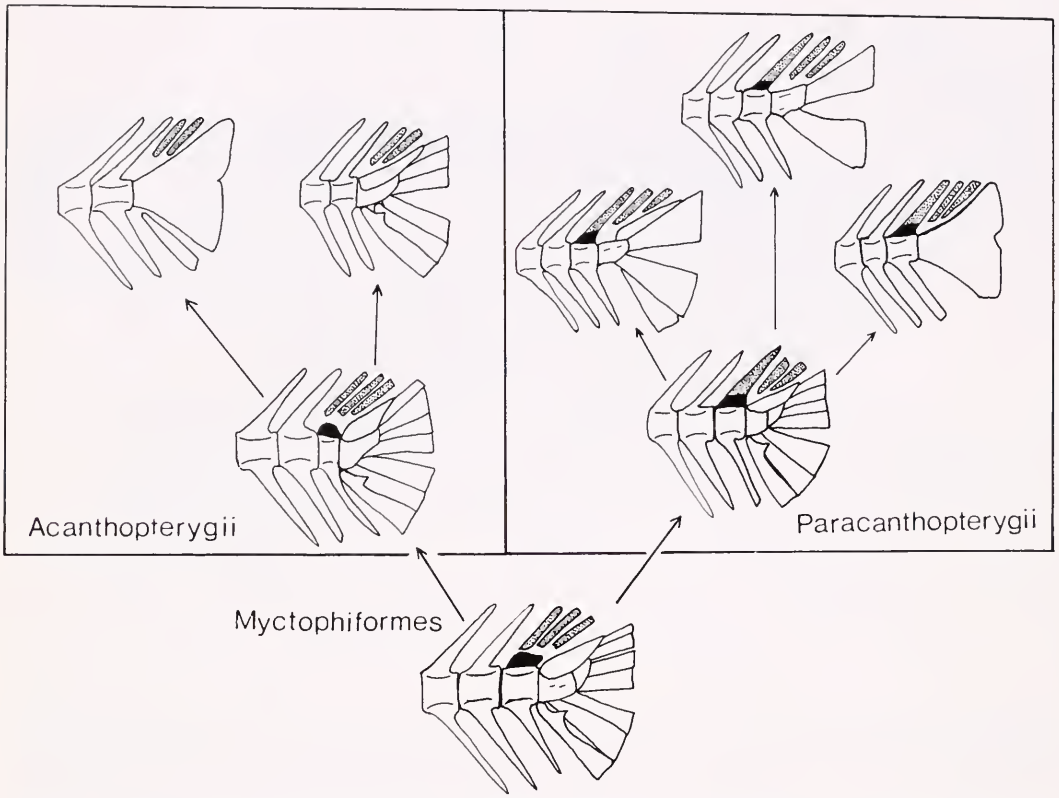


Figure 36. Evolution of the caudal skeleton in the advanced neoteleosts. The arrows connecting the different types indicate possible structural changes, not phyletic lineages. The epurals are stippled, the second preural neural spine crest is black. The primitive configuration of the caudal skeleton is exhibited in the Myctophiformes. In the Paracanthopterygii the most anterior epural fuses with the second preural neural spine crest. Further specializations involve the fusions of the hypurals into platelike elements. In the Acanthopterygii fusions occur of two preural vertebrae, of which one has a complete neural spine and the other a reduced or no neural spine crest. The result of this vertebral fusion is a caudal skeleton configuration which is convergent to that of the Paracanthopterygii. Among more specialized Acanthopterygii fusions occur of the hypurals to form hypural plates.

The Paracanthopterygii is at best an ill-defined group. The pharyngeal jaw apparatus does not furnish any phylogenetic information because in percopsiforms the retractor dorsalis muscle still has two heads, as in myctophiforms, in which the lateral head inserts on the fourth pharyngobranchial. The lateral jaw muscles of paracanthopterygians furnish conflicting evidence. In primitive paracanthopterygians (percopsids and gadids) the maxilla is associated with two muscles, the A_1 and $A_1\beta$. More advanced paracanthopterygians resemble the Myctophidae in having only $A_1\beta$ inserted on the maxilla. The paracanthopterygians were first defined as a superorder (Rosen and Patterson, 1969) on the basis of the structural specialization in the caudal skeleton. In all adult paracanthopterygians the caudal skeleton is characterized by the presence of a full neural spine on the second preural centrum, and two epurals (Fig. 36). Such a structural configuration can be developed by three possible pathways: 1) elongation of a short spine on the second preural centrum, 2) a spineless second preural centrum may fuse with the normally spine-bearing third preural to form a compound centrum with one neural and

two hemal spines, 3) fusion of the first epural with the crest on the second preural centrum. It is hypothesized that in the Paracanthopterygii the third developmental mode has prevailed because the number of epurals is invariabily reduced in the paracanthopterygian caudal skeleton. Paracanthopterygians are tentatively defined by the full neural spine on the second preural centrum thought to be the result of epural fusion, and the presence of not more than two epurals. Unfortunately the question of paracanthopterygian relationships cannot be resolved on caudal evidence. It has been suggested by Rosen (1973) that paracanthopterygians, polymixioids, trachichthyoids and stephanoberycoids are all part of a single monophyletic group in which there are "strong predispositions to develop common features of the head and tail." Polymixioids can also be considered as the primitive sister group of the trachichthyoids plus stephanoberycoids and the paracanthopterygians may be the primitive sister group of all three (Rosen, 1973).

Many paracanthopterygian evolutionary patterns are the reverse of those characteristic of generalized acanthopterygians: 1) a decrease in the depth of the head and trunk, 2) a reduction and eventual loss of median fin spines, 3) an increase in the number of abdominal vertebrae relative to the caudal vertebrae, and 4) a reduction in spiny "ornaments" on the bones of the cheek and operculum.

The precise interrelationships of the paracanthopterygians are still unknown. Consequently we can offer only a tentative scheme of the paracanthopterygian interrelationships leaving many problems unresolved (Fig. 37).

The Percopsiformes. The Percopsiformes, trout perches (*Percopsis*), pirate perches (*Aphredoderus*), and cave fishes (*Amblyopsis*, *Chologaster*), is the only paracanthopterygian group confined to freshwater. It is restricted to North America.

All percopsiforms have a reduced gape of the mouth and reduced oral dentition. In the caudal skeleton there is a sequence of fusions resulting in support of the caudal fin by two large bony plates (fused hypurals) borne on two separate centra. Although median fin spines are either reduced or lost, most percopsiforms have retained spine ornamentation on the head.

The amblyopsids have sensory papillae or tactile organs in very prominent rows on the head, body, and tail. These sensory organs correlate with the lack of vision in the blind species or rudimentary vision in the eyed forms. The distribution of the cave-dwelling amblyopsids is closely correlated with the limestone formations in the central United States (Woods and Inger, 1957).

The Gadiformes. This order includes cods (Gadidae), hakes (Merlucciidae; Marshall, 1966), cusk eels (Ophidiidae), pearlfishes (Carapidae), eel pouts (Zoarcidae), grenadiers and rattails (Macrouridae). With only a few exceptions, members of the Gadiformes are marine. The earliest known gadiforms, from the Eocene, were similar in structure to early percopsiforms, but almost all remained marine and subsequently specialized to inhabit a wide variety of environments.

Gadiforms (Fig. 37) are elongate fishes, often of the deeper and colder dysphotic marine habitats. The tail is reduced or confluent with the long dorsal and anal fins, which have very reduced fin spines. There is also a tendency to develop pelvic fins anterior to (jugular position) the pectoral fins, and mental or circummental barbels. In the upper jaw the postmaxillary process on the premaxilla is distinctly notched (Fig. 38). The brains of more advanced gadiforms have the olfactory lobes located at the olfactory bulb, at a distance from the forebrain (Svetovidov, 1948).

It is postulated that the gadiforms are more closely related to the percopsiforms (Fig. 37) than to any other paracanthopterygian (Rosen and Patterson, 1969), because the two orders share several spe-

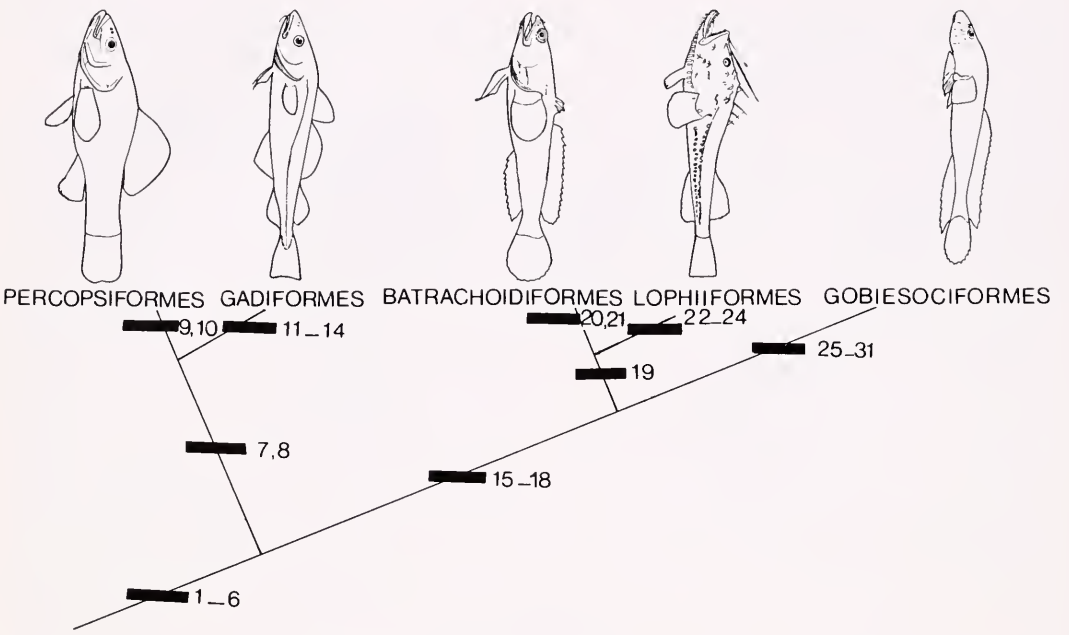


Figure 37. Interrelationships of the major groups of the Paracanthopterygii. Major specializations characterizing the various lineages are: **1,** increase in the number of abdominal vertebrae; **2,** decrease in the depth of the head and trunk; **3,** suboperculum enlarged and operculum reduced; **4,** anterior vertebrae crowded and linked; **5,** trend toward various patterns of fusions of the hypurals; **6,** in the caudal skeleton the second preural centrum possesses a complete spine which is formed by fusion of the first epural with the crest on the 2nd preural centrum; **7,** pterosphenoid and parasphenoid in contact; **8,** olfactory bulb at the olfactory organ and at a long distance from the rest of the forebrain; **9,** in the caudal skeleton there are two large bony plates, representing fused hypurals borne on two separate centra; **10,** reduced gape of the mouth and reduced oral dentition; **11,** postmaxillary process of the premaxilla notched; **12,** tail reduced or confluent with dorsal and anal fins, **13,** pelvic fins in jugular position; **14,** presence of mental barbels; **15,** skull roof flattened; **16,** parasphenoid and frontal bones either approaching each other or sutured to each other; **17,** large sphenotics flaring forward and laterally; **18,** progressive reduction in the ossification of the palatopterygoid; **19,** pectoral radials elongate; **20,** the entopterygoid not ossified; **21,** short spinous dorsal fin and long soft dorsal fin; **22,** modified pectoral girdle correlated with "walking" mechanism; **23,** spinous dorsal fin modified into a lure; **24,** all palatopterygoid bones reduced; **25,** extreme dorsoventral flattening; **26,** joint between cleithrum and supracleithrum; **27,** pelvic fins modified into a sucker; **28,** joint between a convex condyle of interoperculum and concave fossa of epihyal; **29,** hypertrophied sternohyoideus with a medial and lateral head; **30,** asymmetrical heart with reduced sinus venosus and large accessory common cardinal chambers; **31,** short ventral aorta with only three afferent branchial arteries.

cializations which are thought to reflect common ancestry: 1) position of the olfactory lobe at the olfactory organ, and 2) a tendency to establish contacts between parasphenoid and pterosphenoid bones in the skull (Fig. 37: characters 7, 8).

The Gadidae and Merluccidae, containing the cod, haddock, pollock, ling, hake, and whiting, are predominantly cold- and temperate-water groups occurring mostly in the northern hemisphere. Gadids and merluccids share an epihyal-interopercular joint. A medially directed process arises from the medial surface of the interoperculum, and its concave articular surface meets the convex protuberance on the posteroventral corner of the epihyal. The general configuration of the joint shows some resemblance to the epihyal-interopercular joint of the gobiesociforms. However, the relative position and the shape of the articular surfaces of the gadid-merlucciid epihyal-interopercular joint differ from

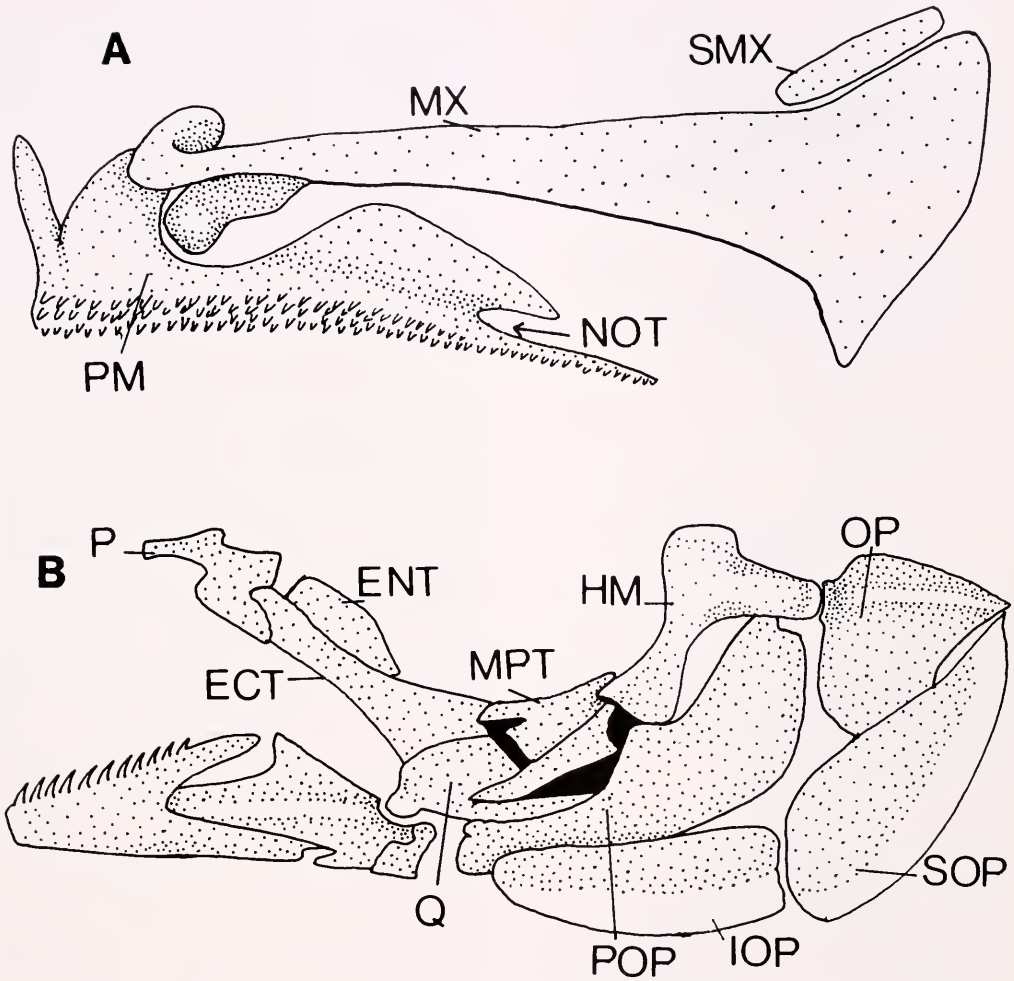


Figure 38. A. Bones of the upper jaw in the gadiform *Ogilbia*. Note the notched postmaxillary process (NOT) of the premaxilla (PM). B. Opercular apparatus and jaw suspension in the gadiform *Pollachius virens*.

Other Abbreviations: ECT, ectopterygoid; ENT, endopterygoid; HM, hyomandibula; IOP, interoperculum; MPT, metapterygoid; MX, maxilla; OP, operculum; P, palatine; POP, preoperculum; Q, quadrate; SMX, supramaxilla; SOP, subopercular.

those of the gobiesociforms. The former represent the world's most valuable food fishes. Many species live near the bottom and utilize the benthic invertebrate fauna as food. Gadids also hold the record for being the most prolific egg producers, a single large female laying around 9,000,000 eggs in one spawning season.

The Macrouridae (rattails; 15 genera and about 250 species) have large heads and eyes, long tapering tails and live in the depths of all the oceans in tremendous abundance (Okamura, 1970). Some of the eelpouts (Zoarcidae) are viviparous, giving birth to as many as 40 young. Zoarcids are common fishes in the cold waters of both the Arctic and Antarctic. Twenty-eight zoarcid genera with 65 species have been described (Nielsen, 1968; McAllister and Rees, 1964). The

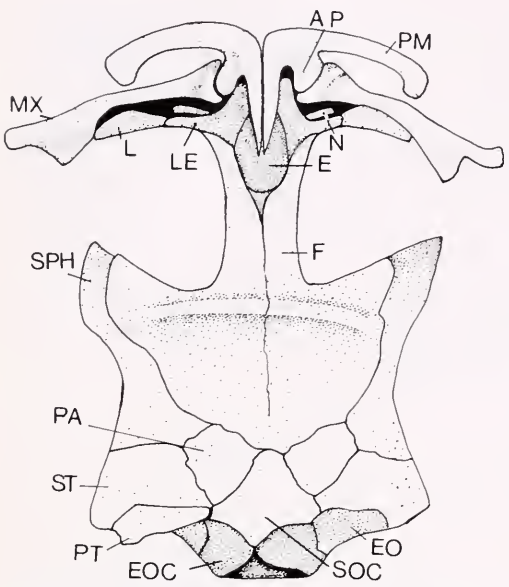


Figure 39. Dorsal view of the skull of *Thalassophryne* to show flattening of the skull and the large, laterally flaring sphenotics (SPH).

Other Abbreviations: AP, articular process of the premaxilla; E, ethmoid; EO, epiotic; EOC, exoccipital; F, frontal; L, lacrimal; LE, lateral ethmoid; MX, maxilla; N, nasal; PA, parietal; PT, posttemporal; SOC, supraoccipital; SPH, sphenotic; ST, pterotic.

Carapidae (pearlfishes) are small fishes that live commonly (some even parasitically) in mollusks and sea cucumbers both in tropical and temperate oceans (Arnold, 1956). The Ophidiidae (brotulas and cusk eels; Nielsen, 1969) contains about 16 genera with 190 species (Gosline, 1971). A specimen of the ophidiid *Abyssobrotula galatheae* has been dredged at a depth of about 8,000 meters which is the deepest record of a captured teleost fish (Nielsen, 1977).

The Batrachoidiform Lineage. This group has diversified into three orders, the Batrachoidiformes, Lophiiformes, and Gobiesociformes (Fig. 37). Four specializations link these three groups together (Fig. 37: characters 15–18). The skull roof is greatly flattened, and the parasphenoid either approaches (Gobiesociformes) or is sutured to (Lophiiformes, Batrachoidiformes) the frontals. With the flattening of the skull the sphenotics have become very large, flaring forward and laterally, while the infraorbital bones are represented only by a lacrimal (Fig. 39). All three groups have well-differentiated ascending processes of the premaxilla and show trends toward a strong connection of the hyomandibula with the preoperculum and reduction in ossification of the palatopterygoid arch.

Key features that relate the batrachoidiform lineages with the gadiforms are found in the gill cover, the anterior vertebral column, the median fins, and skin (Fig. 37: Rosen and Patterson, 1969). In both the gadiforms and batrachoidiform lineages the operculum is reduced, while the sub-operculum has become greatly enlarged, forming most of the distinctly angular gill cover and extending upward and backward to the posterodorsal tip of the operculum (Fig. 38). The anterior vertebrae are not only compressed but are joined via overlapping pre- and postzygapophyses, while the median fins are long and many-rayed, mostly confluent with the caudal except in specialized members. Finally, both lineages have reduced scales or have lost them altogether (Fig. 37).

The three orders within the batrachoidiform lineage differ in a number of structural specializations concerned with feeding and locomotion.

Batrachoidiforms (toadfishes, e.g., *Opsanus*) are primarily coastal benthic fishes of the Atlantic, Indian, and Pacific Oceans. They are first known from the Miocene. Batrachoidiforms are slow-moving bottom fishes with a short spinous dorsal fin and long soft-rayed dorsal fin. In the palatopterygoid arch the entopterygoid is the only element that is not fully ossified. The radial bones (Fig. 40) supporting the pectoral fins are typically elongate. Toadfishes can live out of water, sometimes for hours, and can make sounds, usually grunts, growls, or a single boat-whistle blast. Sound is produced by

specialized "sonic muscles" in association with the swimbladder (Skoglund, 1961). The 55 species of batrachoidiforms are primarily marine benthic fishes, except for two species confined to fresh water.

Lophiiformes, comprising the goosefishes (Lophiidae), anglerfishes (Ceratioidei), frogfishes (Antennariidae), batfishes (Ogcocephalidae; Bradbury, 1980), Tetrabrachiidae, Lophichthyidae, Brachionichthyidae, and Chaunacidae, are widespread marine fishes in shallow water as well as deep-sea habitats (Bertelsen, 1951). In the lophiiforms all pterygoid bones in the palatopterygoid arch are reduced. However, most of the major specializations of lophiiforms concern the feeding mechanism, which in general is adapted to the taking of large prey at high speeds (Grobecker and Pietsch, 1979). Lophiiforms are thought to be monophyletic sharing the following synapomorphies (Pietsch, 1981): 1) Spinous dorsal fin primitively of six spines, the anteriormost three of which are cephalic in position and modified as a luring apparatus; 2) epiotics separated from parietals and meeting on the midline posterior to the supraoccipital; 3) gill opening restricted to a small, elongate, tubelike opening situated immediately dorsal to, posterior to, or ventral to the pectoral base; 4) eggs spawned in a double, scroll-shaped mucous sheath. In the wholly benthic forms, the pectoral girdle is greatly modified in accordance with the development of clasping, prehensile, and "walking" mechanisms. Many members have fewer than five narrow and elongate radials, of which the ventral most is considerably expanded distally. The Lophiiformes comprises 18 families with about 255 species, including numerous highly specialized and bizarre forms. In some families the males are parasitic on the females, attaching firmly with their jaws and becoming, in most cases, completely dependent upon the female for their basic physiological functions (Fig. 37).

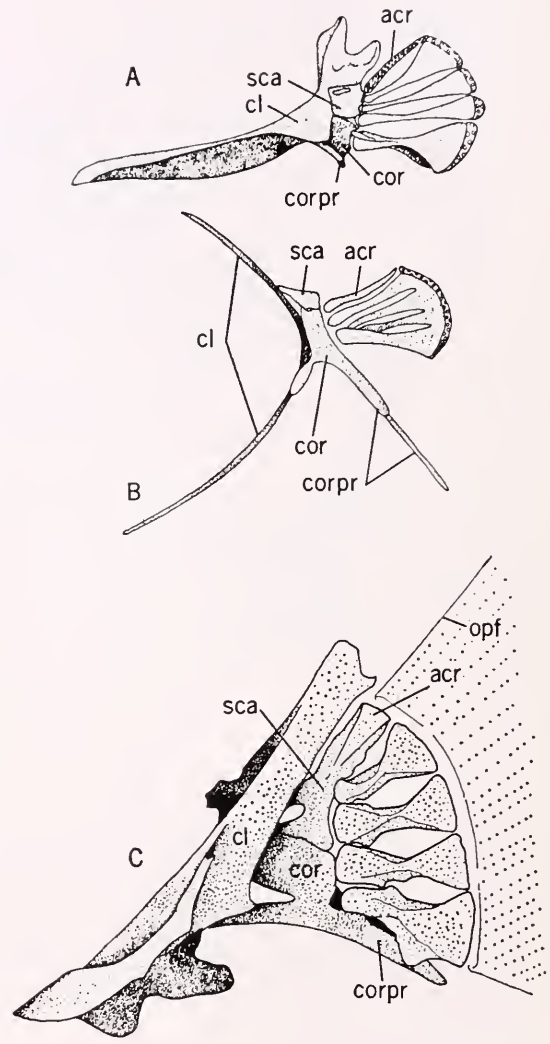


Figure 40. Shoulder girdle in members of the batrachoidiform lineage. A. *Batrachoides*, a batrachoidiform, after Monod (1960). B. *Gigantactis*, a lophiiform, after Waterman (1948). C. *Gobiesox*, a gobiesociform, after Rosen and Patterson (1969).

Abbreviations: acr, accessory upper pectoral radial; cl, cleithrum; cor, coracoid; corpr, posteroventral process of coracoid; opf, outline of pectoral fin; sca, scapula.

Gobiesociforms (clingfishes) are small, dorsoventrally flattened fishes with a ventral sucker formed of the modified pelvic fin and surrounding tissue (Briggs, 1955; Gosline, 1970). They inhabit ma-

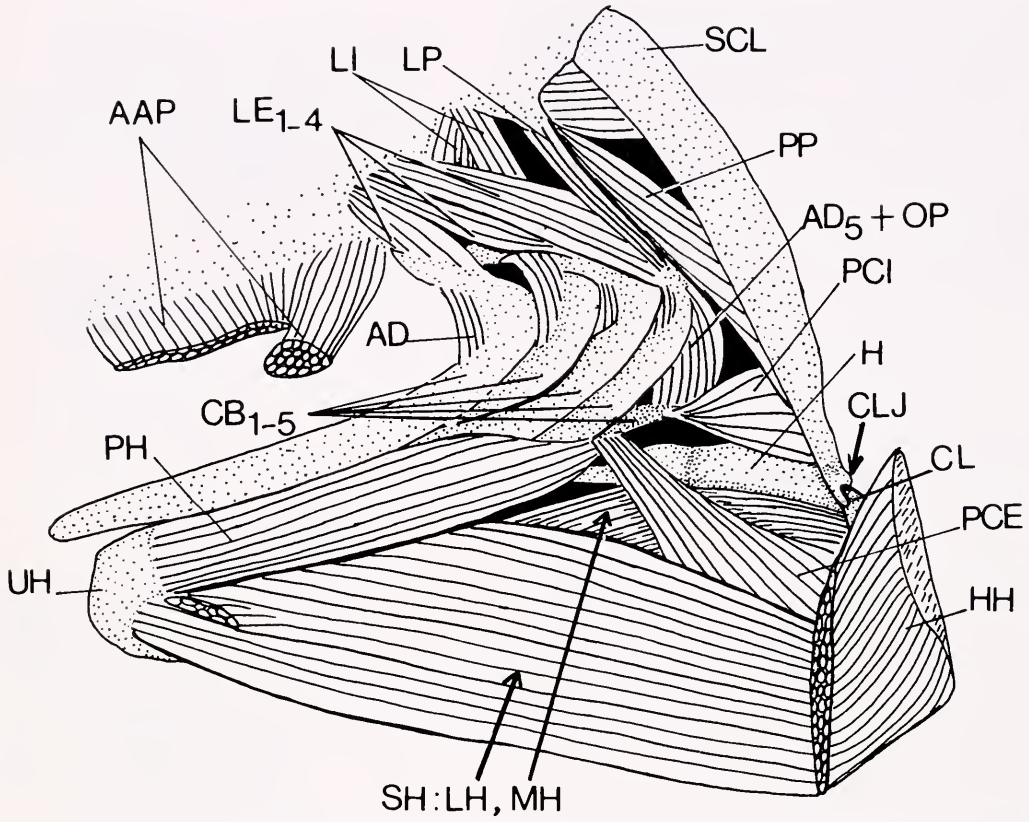


Figure 41. Lateral view of the branchial musculature after removal of the gills and mucous membranes in the gobiesociform *Alabes rufus*. The sternohyoideus (SH) has well-differentiated lateral (LH) and medial heads (MH); the ventral end of the supracleithrum (SCL) forms a distinct joint (CLJ) with the cleithrum.

Other Abbreviations: AAP, adductor arcus palatini; AD, adductor branchialis; AD_5+OP, fifth adductor and obliquus posterior muscles; CB_{1-5}, ceratobranchials 1–5; CL, cleithrum; CLJ, supracleithrum-cleithral joint; H, heart; HH, hyohyoideus, cut and reflected to expose sternohyoideus; LE_{1-4}, levatores externi 1–4; LI, levator internus; LP, levator posterior; OP, obliquus posterior; PCE, pharyngocleithralis externus; PCI, pharyngocleithralis internus; PH, pharyngohyoideus; PP, protractor pectoralis; SH, sternohyoideus with lateral head (LH) and medial head (MH); UH, urohyal.

rine and occasionally freshwaters in the tropics and along many temperate seacoasts. The dorsoventral flattening of the head and body is correlated with the orientation and shape of the bones of the jaw suspension and opercular apparatus. The pterygoid bones in the palatopterygoid arch are lost (Rosen and Patterson, 1969). Most of the specializations of the gobiesociforms correlate with ecological zones involving rapid water exchange, such as the intertidal zone and steeply descending freshwater streams (Fig. 37).

As observed by Springer and Fraser (1976), most of the specialized osteological characters shared by the gobiesociforms are reductional in nature: the loss of scales, basisphenoid, pterosphenoid, metapterygoid, mesopterygoid, suborbitals (except lacrymal), and first infrapharyngobranchial. According to Springer and Fraser (1976), the single most significant synapomorphy of the Gobiesociformes is the presence of a joint between the supracleithrum and the cleithrum: the supracleithrum has a shallow, concave process on its distal end that articulates with a convex condyle on the anterior

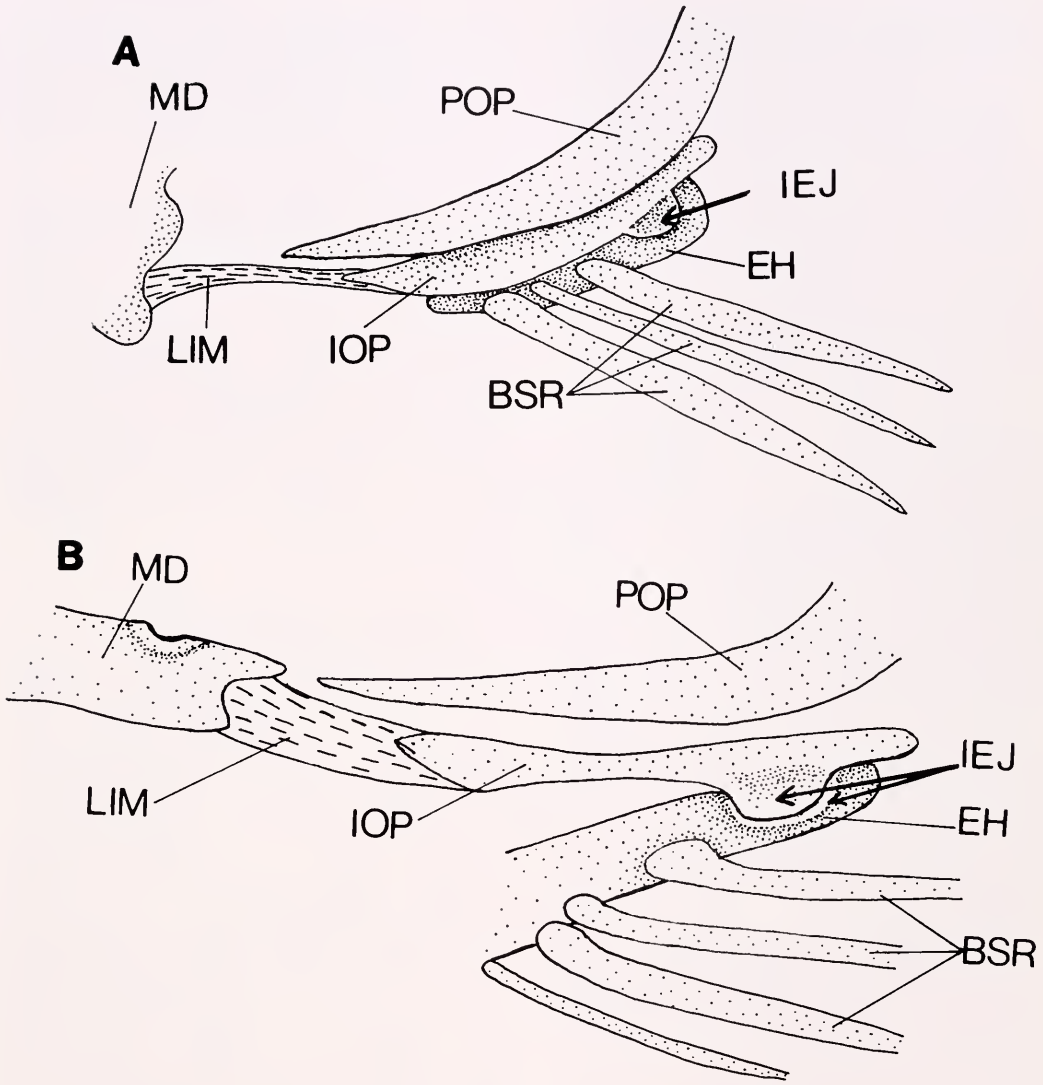


Figure 42. Ventrolateral view of the association of the epihyal (EH) and interoperculum (IOP) of *Alabes dorsalis* (A) and *Gobiesox papillifer* (B) (MCZ 44836). The interoperculum has been dissected away from the preoperculum, and the hyoid ramus pulled down, to reveal the epihyal-interoperculum joint (IEJ).

Other Abbreviations: BSR, branchiostegal rays; EH, epihyal, with a condyle of the interoperculum and a fossa in the epihyal; IOP, interoperculum; LIM, interoperculomandibular ligament; MD, mandible; POP, preoperculum.

surface of the proximal end of the cleithrum (Fig. 41). Such a joint is not duplicated in other fishes. Because *Alabes* (Alabetidae or Cheilobranchidae) possess a similarly specialized supracleithrum-cleithrum joint, it has been placed in the Gobiesociformes (Springer and Fraser, 1976). Previously, the Alabetidae has been classified with the Synbranchiformes (Regan, 1912) or the Blenniidae (Vaillant, 1905; Greenwood, 1975).

We present additional synapomorphies

characterizing the Gobiesociformes as a monophyletic assemblage and offer supporting evidence that *Alabes* is indeed a gobiesociform (Fig. 37: characters 28–31).

Gobiesociforms (including *Alabes*) have a joint between the interoperculum and epihyal bone superficially resembling the condition in gadids and merlucciids. From the medial surface of the interoperculum toward the rear third of the bone, a distinct process arises. The process is directed medially and has a cartilage lined convex condyle, which fits in a matching, shallow concavity on the lateral aspect of the epihyal (Fig. 42). This linkage establishes a firm connection between the epihyal and interoperculum. A second linkage between interoperculum and hyoid is present in the form of a very strong cordlike ligament. The functional significance of this linkage is still unknown, but it is possible that the sternohyoideus-hyoid-interoperculum coupling to open the mouth (Liem, 1970) is dominant in the gobiesociforms, because of the strong double linkages of the interoperculum and the hyoid, and the hypertrophied sternohyoideus muscle with two characteristic heads (Fig. 41): a medial and lateral head, separated by a hypertrophied pharyngocleithralis externus muscle.

Gobiesociforms (including *Alabes*) have a very specialized cardiac morphology not encountered in other teleosts. The heart is distinctly asymmetrical, with the ventricle on the right side and the atrium on the left (Fig. 43). The sinus venosus is greatly reduced, but two large chambers form at the point where the anterior and posterior cardinal veins enter the heart. These accessory common cardinal chambers are much larger than the sinus venosus and bulbus arteriosus. The presence of these accessory common cardinal chambers represents a synapomorphy of the gobiesociforms. Anteriorly the ventral aorta tends to be short and only three afferent and efferent branchial arteries are present. The fourth afferent and efferent branchial arteries are lacking. The first afferent branchial arteries originate independently from the ventral aorta. The second and third afferent branchial arteries originate by a long common root from the ventral aorta (Fig. 43).

The additional synapomorphies given here seem to indicate that the gobiesociforms with the inclusion of the Cheilobranchidae (Alabetidae, with 1 genus *Alabes* and 4 species) is a monophyletic assemblage defined by the presence of a joint between the supracleithrum and cleithrum, a joint between the interoperculum and the epihyal, the accessory common cardinal chambers in the heart, asymmetry of the heart, and the characteristic configuration of the three afferent branchial arteries.

The Acanthopterygii

This vast group of advanced neoteleosts is first known in the Cretaceous. The Acanthopterygii and Paracanthopterygii can be considered members of a monophyletic lineage (Fig. 14) because both groups show strong development of ctenoid scales (already present in the myctophiforms), armored opercular bones, and an elongation of the ascending and articular processes of the premaxilla. Furthermore, in both groups there are evolutionary trends toward an elevation of the pectoral fins on the flank and movement of the pelvic fins anteriorly. These characters, however, are less than satisfactory, and a convincing definition of this lineage is lacking. An obvious feature of generalized acanthopterygians, and the one to which this term refers, is the differentiation of stiff spines in the anal and dorsal fins. This radiation includes the great majority of modern marine fish species as well as a large number of freshwater forms. The acanthopterygians represent a monophyletic group characterized by several major structural and functional specializations. The specialized acanthopterygian char-

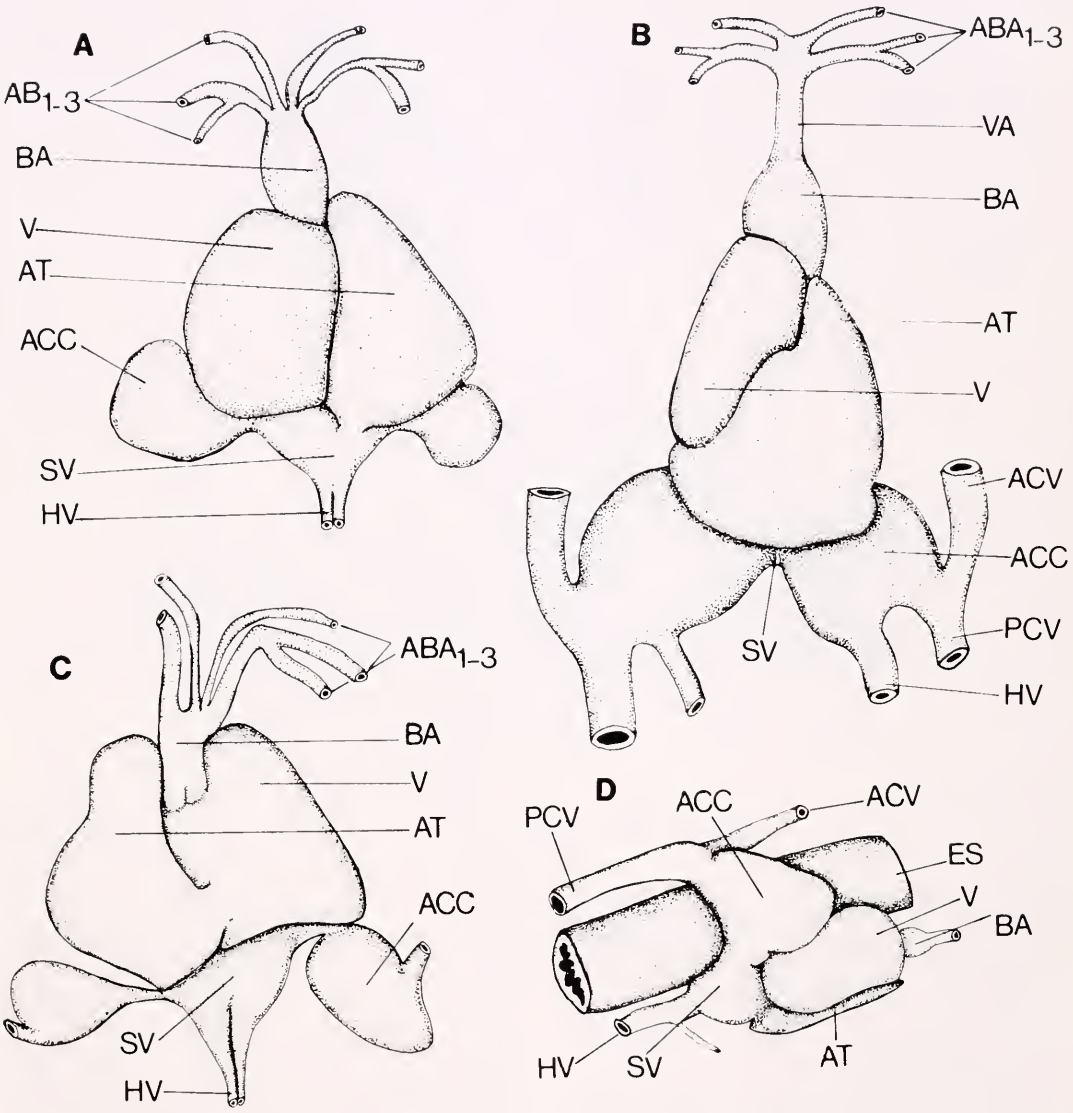


Figure 43. Cardiac morphology in the gobiesociforms *Alabes dorsalis* and *Gobiesox papillifer*. A. ventral view of the heart and great vessels in *Alabes*; B. ventral view of the heart and great vessels in *Gobiesox*. C. dorsal view of the heart and great vessels in *Alabes*. D. lateral view of the right side of the heart of *Alabes*.

Abbreviations: ABA_{1-3}, afferent branchial arteries 1–3; ACC, accessory common cardinal chamber; ACV, anterior cardinal vein; AT, atrium; BA, bulbus arteriosus; ES, esophagus; HV, hepatic vein; PCV, posterior cardinal vein; SV sinus venosus; V, ventricle; VA, ventral aorta.

acter complexes occur in two functional units: the pharyngeal jaw apparatus and the oral jaw mechanism.

The upper pharyngeal jaw apparatus is characterized by a specialized retractor dorsalis muscle (Fig. 44:RD) that inserts principally or entirely on the third pharyngobranchial. In addition, the second and third epibranchials are enlarged, forming the principal structural support

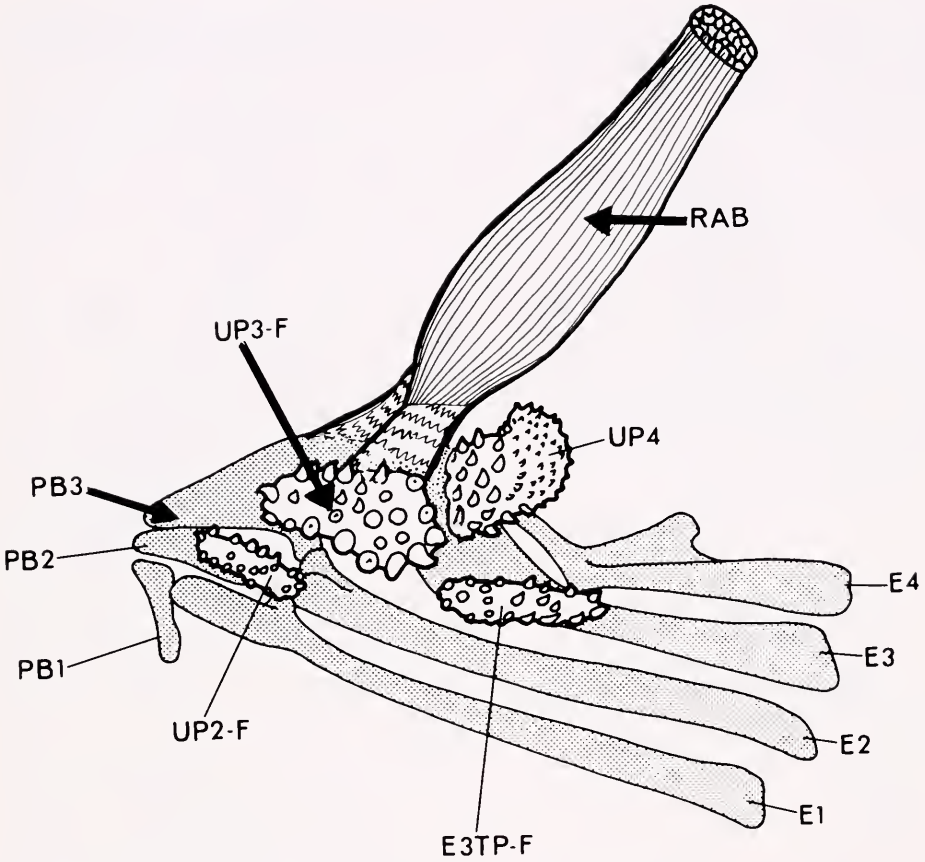


Figure 44. Dorsal gill arch elements and the retractor dorsalis (RAB) muscle in the acanthopterygian *Epinephelus* (ventral view). Muscle is inserted on the upper toothplate (UP3-F) fused to the third pharyngobranchial (PB3).

Other Abbreviations: E_{1-4}, epibranchials; PB_{1-3}, pharyngobranchials; TP-F, toothplate fused to endoskeleton; UP, upper toothplate; UP-F, upper toothplate fused to endoskeleton (Modified from Rosen, 1973).

for the upper pharyngeal jaws (Fig. 44; Rosen 1973).

In myctophiform and paracanthopterygian fishes the upper jaw symphysis is capable of little or no foward movement, while acanthopterygians have a much more mobile upper jaw. With the emergence of a well-developed ascending process on the premaxilla, the symphyseal and alveolar parts of the bone are capable of significant forward displacement or protrusbility (Fig. 45; Alexander, 1967). Upper jaw protrusion in acanthopterygians can be accomplished in at least four different ways (Liem, 1979) and can be modulated precisely by various patterns of muscle contraction. Thus the acanthopterygian jaw apparatus is a prehensile device of great versatility. The structural diversification seen in the acanthopterygian jaw apparatus is great and may be correlated with the multiple kinematic pathways underlying upper jaw protrusion. The 13 orders within the Acanthopterygii may be divided into two groups (categories or series): the Atherinomorpha, and the poorly defined Percomorpha.

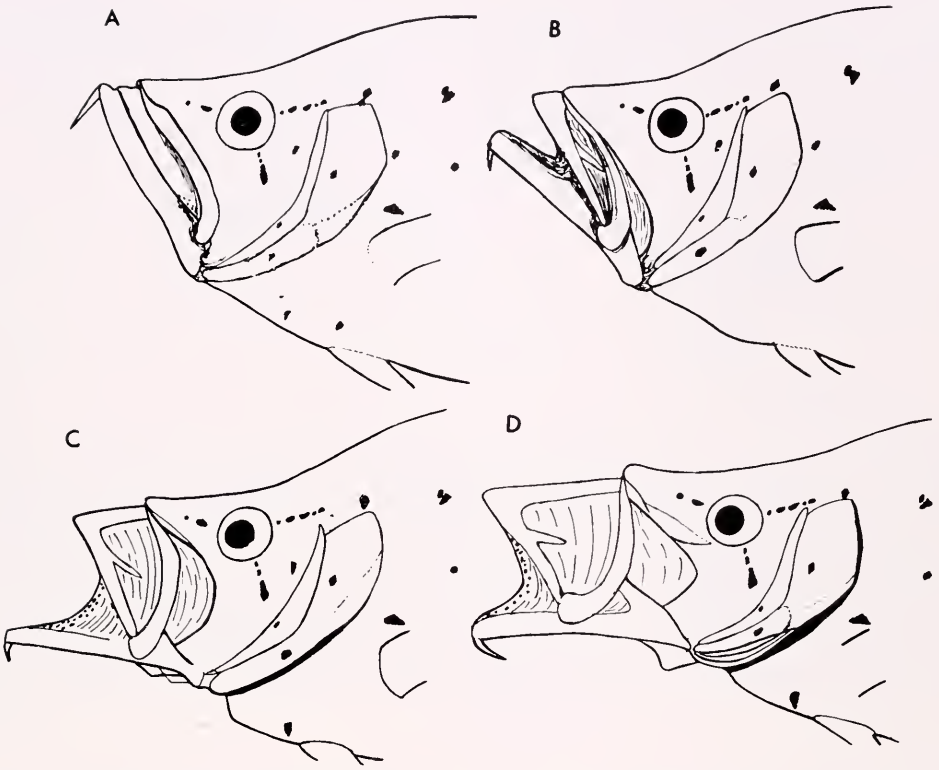


Figure 45. Jaw protrusion in the percoid fish *Monocirrhus* during the capture of prey. A–D. Four representative stages of mouth opening and jaw protrusion. D. fully protruded condition. (From Liem, 1970.)

Atherinomorpha

This group is first known from the Eocene and according to the most recent classification (Parenti, 1981; Rosen and Parenti, 1981) contains 11 families and about 830 species, including the killifishes (cyprinodontids), live-bearing top minnows (Poeciliidae), silversides (Atherinidae), four-eyed fishes (Anablepidae), ricefishes (Adrianichthyidae), halfbeaks (Hemiramphidae), needlefishes (Belonidae), and ocean flying fishes (Exocoetidae). Atherinomorphs have a nearly world-wide distribution and inhabit marine waters and freshwaters both in tropical and temperate climates.

There is considerable evidence that the atherinomorphs are members of a monophyletic assemblage (Rosen and Parenti, 1981) representing a major radiation at the advanced neoteleostean level. Atherinomorphs share, among others, the following derived characters (Rosen and Parenti, 1981): 1) A specialized oral jaw mechanism in which the rostral cartilage is not attached to the premaxilla and the protrusible upper jaw has crossed palatomaxillary ligaments with a maxillary ligament to the cranium. It is postulated that the left and right premaxillae are capable of and normally undergo independent movement during upper jaw protrusion (Rosen, 1964; Karrer, 1967). 2) A large demersal egg with many oil droplets that coalesce at the vegetative pole and rather long adhesive filaments. 3) The absence

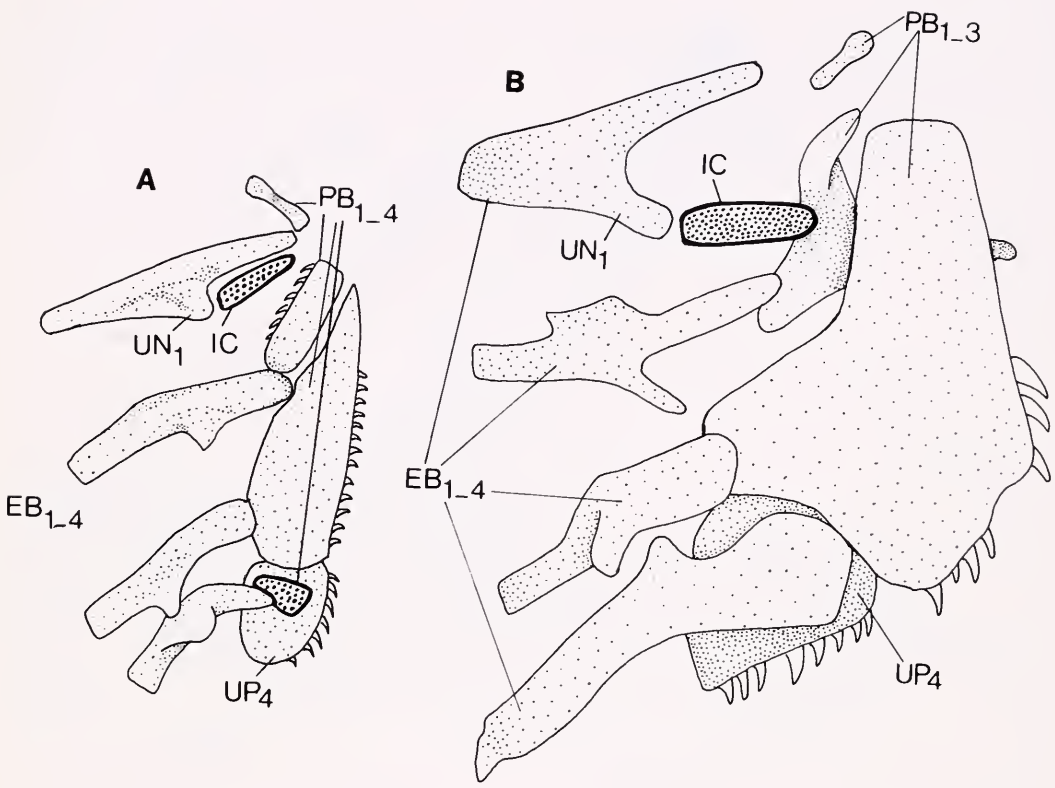


Figure 46. Dorsal gill elements seen from dorsal view. A. Generalized percoid (*Morone*). B. Atherinomorph (*Thelmatherina*). In generalized percoids the fourth pharyngobranchial is present, while in atherinomorphs the element is lost. (Modified from Rosen and Parenti, 1981.)

Abbreviations: EB_{1-4}, epibranchials 1–4; IC, interarcual cartilage; PB_{1-4}, pharyngobranchials 1–4; UP_4, upper toothplate of fourth branchial arch.

of the third, fourth, and fifth infraorbital bones and the fourth pharyngobranchial (Fig. 46; Rosen and Parenti, 1981).

The relationship between atherinomorphs and the Percomorpha is specified by the presence in the dorsal gill arch skeleton of an interarcual cartilage between the first epibranchial and second pharyngobranchial (Fig. 46; Rosen and Parenti, 1981); however, see Travers (1981) for the distribution of the interarcual cartilage. Atherinomorphs have four bladelike branchiostegals inserting laterally on the hyoid bar, the anteriormost located just posterior to a notch on the anterior ceratohyal.

Included in the Atherinomorpha are the "atherinoids" (Atherinidae, Bedotiidae, Isonidae, Melanotaeniidae, Phallostethidae, and Telmatherinidae), the Cyprinodontiformes (Parenti, 1981), and the Beloniformes (Adrianichthyoidei and Exocoetoidei).

Within the atherinomorphs, the "atherinoids" are still problematic since they cannot be regarded as a monophyletic group, and at present the Atherinoidei cannot be characterized. Among the atherinoids are the Atherinidae (silversides) most of which are marine. However, many species live in freshwater (Barbour, 1973). The grunion, *Leuresthes tenuis*, is probably the best known atherinid because of its peculiar spawning behavior which is

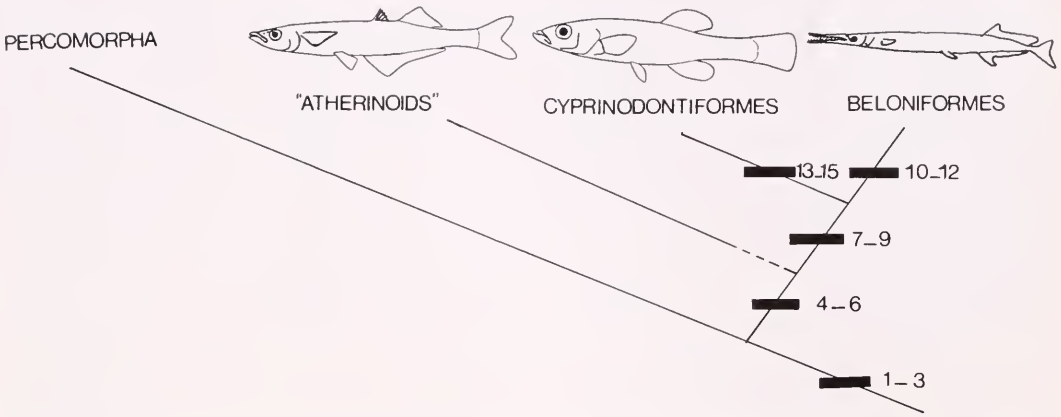


Figure 47. Phylogenetic relationships of the Atherinomorpha. Note that, at present, the Percomorpha are not characterized by any shared derived character(s). The "Atherinoids" are probably not monophyletic, since they lack unifying specialized characters. **1,** presence of an interarcual cartilage in the dorsal gill arch skeleton between the first and second pharyngobranchial; **2,** retractor dorsalis inserts principally or entirely on the third pharyngobranchial; **3,** symphyseal and alveolar parts of the premaxilla are capable of significant downward and forward displacement; **4,** a specialized oral jaw mechanism in which the rostral cartilage is not attached to the premaxilla and the protrusible upper jaw has crossed palatomaxillary ligaments with a maxillary ligament to the cranium; **5,** a large demersal egg with many oil droplets and adhesive filaments; **6,** the third, fourth, and fifth infraorbitals and the fourth pharyngobranchial are absent; **7,** the first epibranchial has an expanded base; **8,** second and third epibranchials reduced; **9,** 1st and 2nd infraorbital lacking; **10,** symmetrical internal skeleton of the caudal fin; **11,** caudal fin is not lobed; **12,** low-set pectoral fins associated with a large, scalelike postcleithrum; **13,** presence of a large ventral flange on the fifth ceratobranchials; **14,** second and third epibranchials distinctly smaller than other epibranchials; **15,** second pharyngobranchial vertically reoriented.

determined by the lunar cycle (Clark, 1925; Walker, 1952). More than 150 atherinid species belonging to 29 genera have been described. The rainbow fishes (Melanotaeniidae) inhabit freshwaters of Australia, Aru Island, and New Guinea. The Phallostethidae are peculiar atherinoids possessing highly specialized, muscular and bony copulatory organs under the throat of the male (Bailey, 1936; Roberts, 1971a, b).

The remaining two atherinomorph lineages are the Cyprinodontiformes and Beloniformes (Fig. 47) which share several specialized characters in the dorsal gill arches (Fig. 48): 1) the first epibranchial has an expanded base, 2) the second and third epibranchial are reduced, and 3) the first pharyngobranchial and the second infraorbital bone are lost.

Beloniformes are readily characterized by the presence of a large ventral flange on the fifth ceratobranchial, relatively small second and third epibranchials, a vertical reorientation of the second pharyngobranchial and the loss of the interhyal.

The beloniforms are composed of the exocoetoids, characterized by a median lower pharyngeal toothplate (Rosen, 1964) and more than three anterior branchiostegal rays, and the Adrianichthyoidei with a greatly expanded articular surface of the fourth epibranchial and the loss of the metapterygoid or ectopterygoid. Among the exocoetoids (Karrer, 1967) are the marine flying fishes (Exocoetidae), the marine and freshwater halfbeaks (Hemiramphidae), the predominantly marine needlefishes (Belonidae), and the marine sauries (Scomberesocidae). The adrianichthyoids contain one family, the Adrianichthyidae (which includes the Oryziidae and Horaichthyidae). The medakas (*Oryzias*) from the fresh- and brackish waters of India and Japan to the Indo-

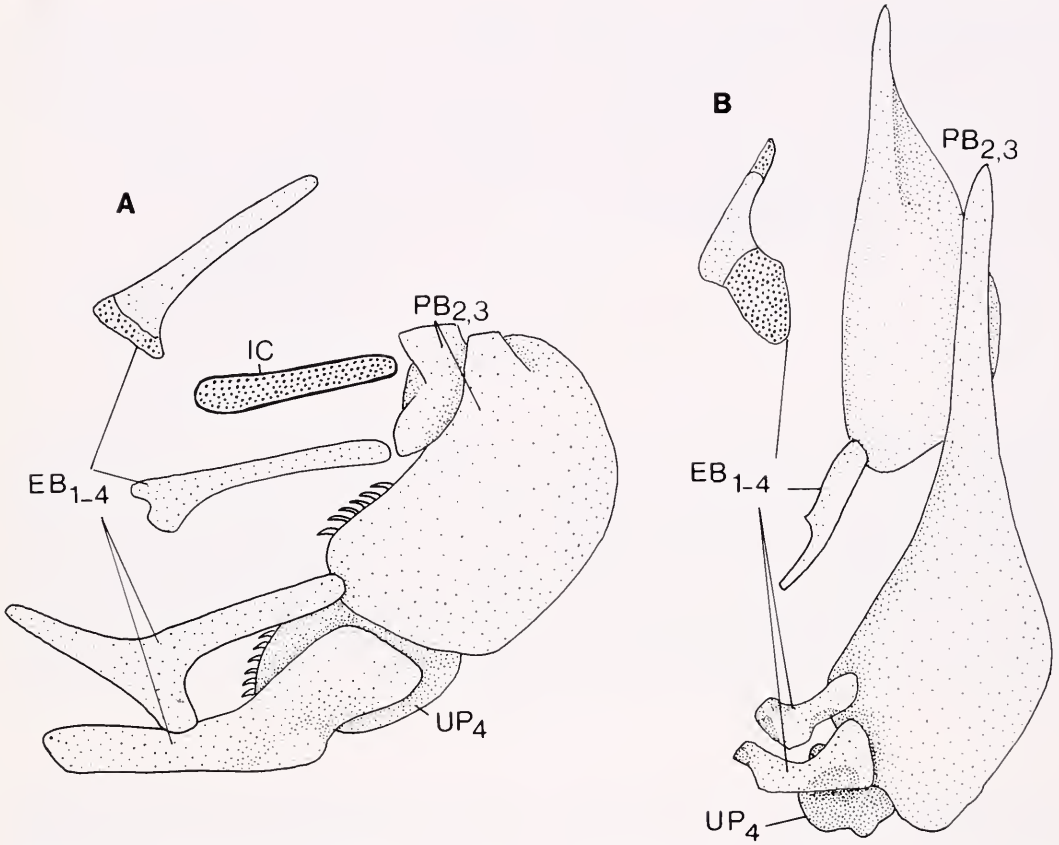


Figure 48. Dorsal gill arch elements seen from dorsal view. A. Representative cyprinodontiform (*Aplocheilus*). B. Representative beloniform (*Xenentodon*). (Modified from Rosen and Parenti, 1981.)

Abbreviations: EB_{1-4}, epibranchials 1–4; IC, interarcual cartilage; $PB_{2,3}$, pharyngobranchials 2, 3; UP_4, upper toothplate of fourth branchial arch.

Australian Archipelago, are often used for developmental studies.

Cyprinodontiforms are characterized by several unique features (Parenti, 1981): 1) the internal skeleton of the caudal fin is symmetrical because the epural symmetrically opposes the parhypural, 2) the unlobed caudal fin, and 3) the low-set pectoral fins with a large, scalelike postcleithrum. In general, cyprinodontiforms have a pattern of early sexual maturation and prolonged embryonic development. In the most recent classification (Parenti, 1981), nine families are recognized within the cyprinodontiforms. Quite a few have served as exemplary experimental subjects and many are very popular with aquarists. Among the killifishes are annual fishes with eggs that can withstand dessication and possess different developmental rates so they can survive unpredictable fluctuations in the environment (Wourms, 1972). One of the best known members of the neotropical Rivulidae is *Rivulus marmoratus*, the self-fertilizing hermaphroditic species (Harrington, 1961). The four-eyed fishes (Anablepidae) of the freshwaters of southern Mexico to northern South America have their cornea and retina divided into up-

per and lower "eyes," the upper eye above the waterline serving for aerial vision. Among the Poeciliidae and lampeyes (*sensu* Parenti, 1981) are the famous guppy, *Poecilia reticulata*, and the mosquitofish (*Gambusia affinis*). The upturned mouth opening serves to exploit the oxygen-rich surface layer for respiration. Contrary to common belief, guppies are not surface feeders, but feed on benthic detritus, invertebrates, and algae (Dussault and Kramer, 1981). *Poeciliopsis* is another cyprinodontoid genus which has an all-female species in northwestern Mexico (Schultz, 1973). *Poecilia formosa* consists almost exclusively of females using males of another species (which contribute nothing to the gene pool of the offspring) to stimulate development of the egg. Other cyprinodontiform families are the Old World Aplocheilidae (of which many members are often brightly colored and are popular in the aquarium trade), the viviparous Goodeidae from the freshwaters of west central Mexico (Miller and Fitzsimons, 1971), the Profundulidae, and the Fundulidae of which the brackish water species *Fundulus heteroclitus* is well known to experimental biologists. It is not only very common on the coast of the northeastern U.S. (Bigelow and Schroeder, 1953) but is a very hardy fish with interesting developmental and physiological features.

Percomorpha

The remaining groups in the Acanthopterygii belong to the Percomorpha. The percomorphs are ill-defined (Rosen, 1973) and their internal classification is very tentative, confusing, and problematic. Existing "phylogenetic" schemes are at best grade classifications adopted as temporary expedients. It is certain that many of the major taxa are polyphyletic groups that simply link most of the "primitive" members of a phyletic unit. Forthcoming investigations of phylogenetic relationships based on rigorous and objective approaches and principles will doubtless generate new schemes that depart radically from existing ones. It is almost certain that the Beryciformes and Perciformes are polyphyletic assemblages. Since they occupy key positions in the present scheme, any change in their phylogenetic schemes will greatly affect the classification of the other percomorphs. The classification offered here will serve to identify the weaknesses in our current knowledge of the evolutionary relationships among the percomorphs.

The Beryciformes

Beryciforms are abundant and diverse in the fossil record of the Cretaceous (Patterson, 1964, 1967, 1968b). These primitive marine acanthopterygians include the squirrelfishes (Holocentridae), alfonsinos (Berycidae), lantern-eye fishes (Anomalopidae), and pinecone fishes (Monocentridae) (Zehren, 1979; Woods and Sonoda, 1973). Beryciforms exhibit all the major features that characterize the Acanthopterygii, but, as one might expect in a "basal" group, they differ from more advanced orders by the retention of such primitive features as an orbito-sphenoid bone in the neurocranium, the presence of 18 or 19 rays in the tail fin, the full complement of three epurals, and a low crest on the second preural vertebra in the caudal skeleton. All beryciforms share a peculiar specialization in the tail: the presence of true, unpaired procurrent caudal fin spines (Fig. 49), rather than unsegmented bilaterally paired rays as in other acanthopterygians (Patterson, 1968b); but see Rosen, 1973, page 452 for contradictory observations.

The beryciforms and perciforms appear to share a common ancestry, and the Beryciformes may represent the primitive sister group. Both taxa have the pelvic girdle firmly joined to the pectoral girdle, pelvic fins with a spine and five soft rays, and the second circumorbital bone with a suborbital shelf underlying the eye (Fig. 50). There is little doubt that

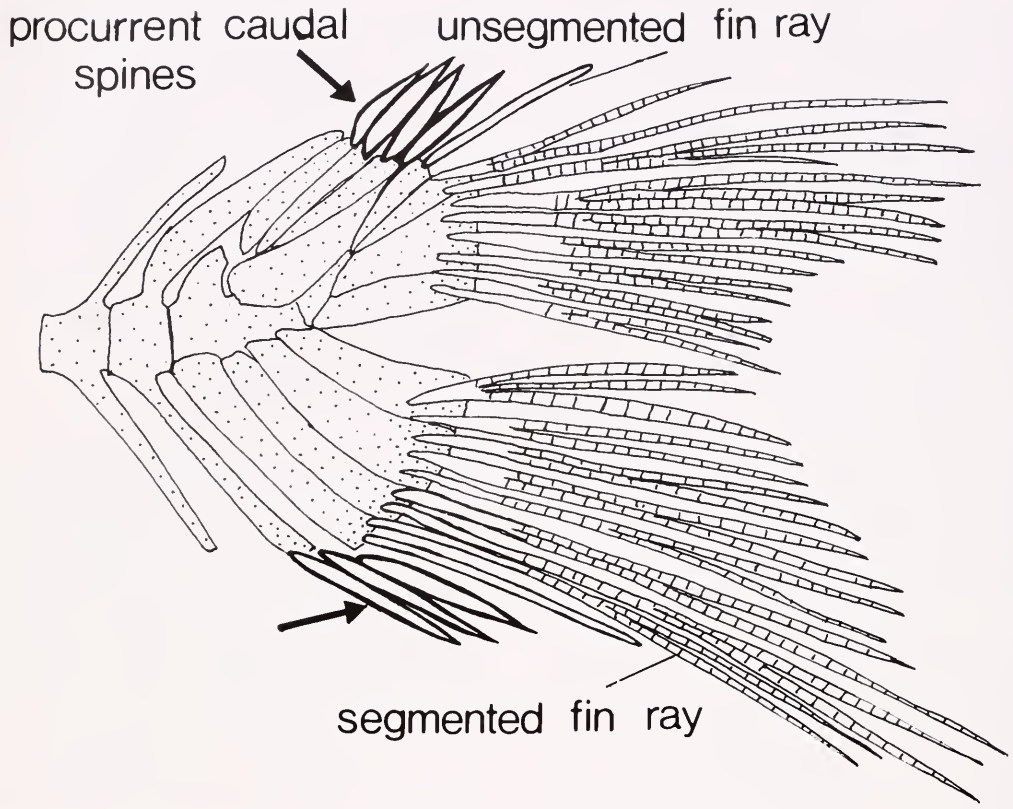


Figure 49. Lateral view of the caudal skeleton of a beryciform, showing the characteristic unpaired, truly spinous structures: the procurrent caudal spines.

these features reflect close phylogenetic relationships between the beryciforms and the largest known order, the Perciforms (perchlike fishes).

Based on the specialized morphology of the otoliths (Fig. 51), Patterson (1964) suggested that the order Zeiformes (dories) is a sister group of the Beryciformes and that both groups are the sister group of the perciform assemblage.

In spite of the extensive and excellent osteological studies by Zehren (1979) and Patterson (1964) the monophyly of the Beryciformes has yet to be demonstrated. All recent beryciform families may represent monophyletic groups (Zehren, 1979). The Monocentridae (pinecone fishes) have a body armor of thick scales and the dentary has a distinct notch on the ventral border. Lantern eye fishes (Anomalopidae) have the anterolateral portions of the nasal prolonged into a distinct process which articulates with the lateral ethmoid and a subocular light organ. In the Berycidae (alfonsinos) the lacrimal is extended posteriorly below infraorbital 1 to articulate with infraorbital 2. Squirrelfishes (Holocentridae) possess a transverse crest on the dorsal surface of the supraoccipital. Other beryciform families are the Trachichthyidae (slimeheads), Diretmidae, Polymixiidae, Gibberichthyidae, Stephanoberycidae (pricklefishes), and Anoplogasteridae (fangtooths). By virtue of their possible sister group relationship to the Perciformes, and uncertainty over their interrelationships, the Beryciformes offer nu-

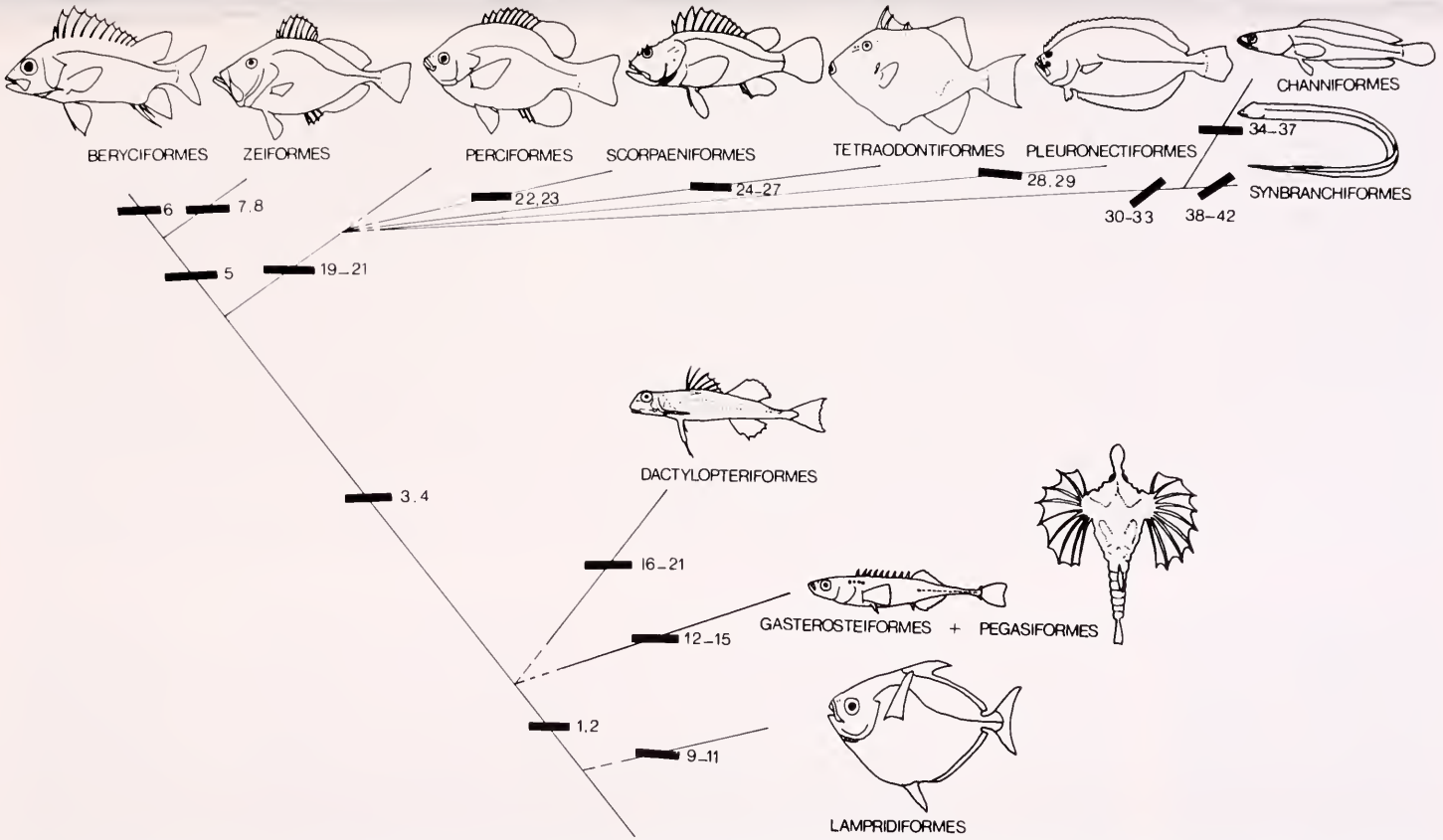


Figure 50. Interrelationships of the major groups of the percomorph Acanthopterygii. Major specializations characterizing the various lineages are: **1,** separate soft and spinous dorsal fins; **2,** pelvic girdle attached to cleithrum; **3,** second circumorbital bone with subocular shelf; **4,** pelvic fin with spine and five rays; **5,** sacculith (otolith) morphology specialized (Fig. 51); **6,** presence of specialized procurrent caudal spines; **7,** decrease in number of vertebrae; **8,** deepening of the body; **9,** maxilla slides out with premaxilla during jaw protrusion; **10,** no true spines in fins; **11,** pelvic girdle attached to a large specialized hypocoracoid; **12,** body encased in bony armor; **13,** small mouth at end of tubular snout; **14,** number of branchiostegals reduced (1–5); **15,** trend to either reduce or modify gills; **16,** no lateral line; **17,** enlarged pectoral; **18,** body covered with scutelike scales; **19,** no free second ural centrum; **20,** 17 principal caudal rays; **21,** caudal skeleton with 5 hypurals; **22,** hypurals fused into two distinct, large plates; **23,** third circumorbital bone with an extension attached to the preoperculum; **24,** entire branchiostegal region covered by a thick layer of scaleless or scaled skin, **25,** no suborbitals, parietals, nasals, sensory canals in the skull, and anal spines; **26,** gill opening restricted to a very small slit just below the base of the pectoral fin; **27,** specialized dermal protective devices; **28,** median fins extend along much of body profile; **29,** bilateral asymmetry affecting topography of the eyes and coloration; **30,** hemispheres of forebrain coalesced (Fig. 60); **31,** adductor mandibulae complex with specialized A_1 and A_2 divisions (Fig. 61); **32,** fourth branchial arteries modified; **33,** fins without spines; **34,** otic bullae for sacculith, utriculith and lagenolith are contained in the prootic bone; **35,** metapterygoid with prominent anterodorsally directed uncinate process; **36,** two ventral aortae emerge separately from the bulbus arteriosus; **37,** gas exchange with air in the suprabranchial and buccopharyngeal cavities, which remain in open communication throughout the breathing cycle; **38,** frontals turned down and sutured to basisphenoid; **39,** large parietals meet in midline; **40,** suspensorium articulates with basisphenoid, frontal, vomer and lateral ethmoids; **41,** interarcual cartilage ossified; **42,** the elongate heart is located far posteriorly in the body cavity. (Many of these characters, e.g., 1–3, 10, and 17, are poor and considerable future work will be necessary to clarify the relationships of the Acanthopterygii.)

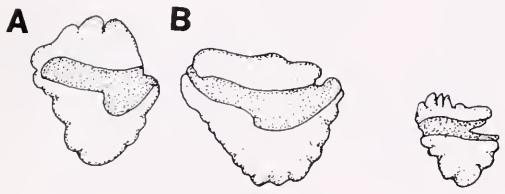


Figure 51. Inner face of the sacculith (otolith with the sacculus). A. The most primitive zeiform *Antigonia*. B. The berycoid *Beryx*. C. The zeiform *Capros*. (Modified from Stinton, 1967.)

merous challenging phylogenetic and evolutionary problems for future workers.

The Lampridiformes

Although the main radiation of acanthopterygian fishes occurs in the Perciformes, there seem to have diverged, at an early stage, an assemblage of odd types of percomorphs. The highly specialized Lampridiformes (opahs) are an assemblage of mainly deep sea fishes (Walters, 1960; Walters and Fitch, 1960). The lampridiform caudal skeleton shows similarities to that of some beryciformes. The proposed relationships of the Lampridiformes to other percomorphs is depicted in Figure 50. Lampridiformes have no true spines in their fins and possess an unusual jaw mechanism in which the maxillae slide out with the premaxillae during protrusion (Oelschläger, 1978; Pietsch, 1978a). The pelvic girdle is not attached to the cleithrum, but instead it is connected to a greatly enlarged special bone of the pectoral girdle, the hypocoracoid (Oelschläger, 1978). *Lampris*, the opah or moonfish, is perhaps the best known for its odd appearance and size (about 1 m, and 300 kg).

The Zeiformes

The dories (Zeidae) and boarfishes (Antigoniidae) together are considered the sister group of the beryciformes (Fig. 50) because of the shared specializations in the morphology of the otoliths (Patterson, 1964). In zeiforms, the caudal skeleton has specialized along the lines characteristic for the perciforms and the zeiform pelvic fin with one spine and five to nine branched rays also approaches the perciform condition. The dories (*Zeus*) are thin, deep-bodied fishes with enormously distensible jaws set at an oblique angle. They are marine and widespread (Myers, 1960).

At this point it seems appropriate to observe that important changes in methods of locomotion have taken place during the evolution of the acanthopterygian fishes. The pattern in the Beryciformes, Lampridiformes, and Zeiformes (Fig. 50) is toward a shortening and deepening of the body with a decrease in the number of vertebrae. The pectoral fins are almost always well developed and are located, possibly for maneuverability, high up on the side of the body. The pelvic fins have moved forward to a position below the pectorals, with the pelvic girdle attached to the cleithrum. Such a forward shift may serve as an aid toward proper balance necessitated by the upward move of the pectorals. The end results of this trend are especially discernable among the Perciformes (Fig. 50).

The Gasterosteiformes

The Gasterosteiformes appear to be another highly specialized side branch of early acanthopterygians (Fig. 50). Pietsch (1978b) has included the former order Pegasiformes in the Gasterosteiformes on the basis of some shared specializations in the feeding apparatus. We follow the provisional phyletic scheme proposed by Pietsch and have put the sea moths (pegasoids), the sticklebacks (Gasterosteidae), sea horses (Syngnathoidei), and trumpet fishes (Aulostomidae, Fistularidae) in a presumably monophyletic assemblage, the Gasterosteiformes.

The Gasterosteiformes are first known from the Lower Eocene and are widely distributed today in both marine and

freshwaters. In this group the body is typically elongate and slender and may be encased in bony plates; the small mouth is usually located at the end of a tubular snout. All members are slow-moving fishes. The sticklebacks (Gasterosteidae) are famous for the numerous studies made on their behavior and physiology (Wootton, 1976).

Because the Gasterosteiformes are so specialized they provide little evidence of their phylogenetic position. In all gasterosteiformes the spinous and soft parts of the dorsal fin are separated. In the pegasoids the pelvic girdle is attached to the cleithrum, and they possess a pterygiophore in the dorsal fin indicating that the spinous dorsal fin has been lost secondarily. It is postulated that in gasterosteids the pelvic girdle has lost its attachment with the cleithrum secondarily. Monophyly of the Gasterosteiformes has not been convincingly demonstrated (Gosline, 1971; Greenwood *et al.*, 1966). Some authors (e.g., McAllister, 1968; J. Nelson, 1976) prefer to recognize two groups at the ordinal level, i.e., Syngnathiformes and Gasterosteiformes. In the Gasterosteidae (sticklebacks) and the Aulorhynchydae (tubesnouts) the postcleithrum is lost. The loss of the postcleithrum is a derived character, suggesting a closer relationship between the Gasterosteidae and Aulorhynchidae than to any other gasterosteiform.

The remaining gasterosteiformes have lost all infraorbitals except for the lacrimal and possess very specialized tufted lobelike gills (Rauther, 1937). Included in this group are six families. The tropical marine trumpetfishes (Aulostomidae) which inhabit reefs and often rest with their bodies in a vertical position with the head downward. The Fistularidae (Cornetfishes) are also tropical marine fishes with exceptionally long tubular snouts (Jungersen, 1910) functioning as pipettelike suction devices. Snipefishes (Macrorhamphosidae) and ghost pipefishes (Solenostomidae) are both small families of mainly tropical marine fishes. The shrimpfishes (Centriscidae) have a peculiar locomotor mode: they swim in a vertical position with the snout downwards. The Syngnathidae (pipefishes and seahorses) are mostly marine fishes inhabiting shallow waters. In syngnathids the males care for the brood the females attach to them in a pouchlike structure or on the ventral surface of the trunk or tail.

The Dactylopteriformes

The Dactylopteriformes (flying gurnards) is a small order of specialized tropical marine fishes (Fig. 50) whose relationships are still unknown. The dactylopteriforms have large pectoral fins giving them an ability to "glide" in a way paralleling the exocoetids or true flying fishes. The dactylopteriforms have the pelvic girdle attached to the cleithrum, and have lost the lateral line. The spinous and soft dorsal fins are separated. Dactylopterids are benthic fishes that can "walk" on the sea floor by alternately moving the pelvic fins (J. Nelson, 1976).

The Perciformes

The order Perciformes (perchlike fishes) cannot be defined cladistically and is almost certainly a gradal and unnatural assemblage. Even though the Perciformes is clearly polyphyletic, many attributes have been assigned to the group: 1) It is the most diversified of all fish orders, 2) It is the largest vertebrate order comprising about 20 suborders containing 150 families and at least 6,900 species, 3) Perciforms dominate vertebrate ocean life and also form a major component of the fish fauna in many tropical and subtropical freshwaters, and 4) It is the basal evolutionary group from which numerous other groups are believed to have been derived (Gosline, 1968). None of the above-mentioned attributes commonly ascribed to perciforms in evolutionary discussions is meaningful because mon-

ophyly of the group has not been established. If the Perciformes is polyphyletic, no statements can be made about their morphological, functional, and taxonomic diversity, evolutionary patterns, evolutionary rates, biogeography, and ecological dominance in the oceans and freshwater. It is better to refrain from perpetuating such evolutionary scenarios so prevalent in the present ichthylogical literature and to focus on the problems and inconsistencies of the internal classification of the Perciformes, and offer hypotheses of relationships of some of the major taxa. Because the Perciformes is presently ill defined and the internal classification so poorly known, this discussion will focus on some specific problems rather than offer a general classification of over 150 families.

To date the Perciformes cannot be defined by either a single specialized character or a combination of specialized characters. The perciform categories discussed below do not necessarily delimit monophyletic groups.

Suborder Percoidei. The most generalized and several specialized perciforms are included in this undefined assemblage. Included in the Percoidei are such important food fishes as the Serranidae (Smith, 1971; Gosline, 1966), the seabasses, with about 370 species of which many are protogynous hermaphrodites (Smith, 1965); the Carangidae, jacks and pompanos with their distinctly compressed bodies; the Mullidae, goatfishes, with their two long chin barbels used for detecting food; the Lutjanidae (Johnson, 1980), snappers, which are sometimes responsible for ciguatera or fish poisoning. Other percoids include the Pomadasyidae (grunts) and Sciaenidae (drums and croakers; Trewavas, 1977), which make sounds, using the swimbladder as a resonating chamber; the wide-spread remoras (Echeneidae; Gosline, 1971) in which the spinous dorsal fin is transformed into a sucking disc; and the Coryphaenidae (dolphins, mahi mahi; Gibbs and Collette, 1959), which are composed of very fast swimming, streamlined oceanic fishes. More generalized percoids include the Centropomidae (Greenwood, 1976), the snooks; the Percidae (Collette, 1963) the perches and darters; and the Centrarchidae, the sunfishes. Many percoid families are strictly marine, e.g., the Grammistidae (soapfishes), Chaetodontidae (butterflyfishes); Kyphosidae (sea chubs), Ephippidae (bonnetmouths); Bramidae (Mead, 1972), pomfrets; Pomatomidae (bluefish); Branchiostegidae (tilefish); Apogonidae (cardinalfishes, Fraser, 1972); Priacanthidae (bigeyes); Teraponidae (tigerperches, Vari, 1978), Grammidae (basslets); Plesiopidae (roundheads); and Leiognathidae (ponyfishes).

Some of the percoid families are thought "to have given rise" to the derived perciform suborders. For example, the Nandidae (leaf fishes) has been hypothesized to be related to the Anabantoidei (Nelson, 1969a; Gosline, 1971). Liem and Greenwood (1981), have argued that the evidence for such a close relationship is questionable. On the basis of functional morphological data it has been shown that the features associated with the tongue-parasphenoid bite in pristolepids are specialized and unique, making them autapomorphic for *Pristolepis*, an important taxon in efforts to relate Nandidae with the Anabantoidei. The dentition on the parasphenoid, basihyal, and third hypobranchial and all features associated with the swallowing apparatus in nandids and channiforms are primitive, and do not indicate relationships with either *Pristolepis* or the Anabantoidei. Thus, the efforts to demonstrate monophyly of the Nandidae, Anabantoidei and Channiformes have failed. However, Barlow *et al.* (1968) and Liem and Greenwood (1981), have discovered evidence that *Badis badis*, which is traditionally classified with or very near the Nandidae (Gosline, 1971) may share specializations with the Anabantoidei: a

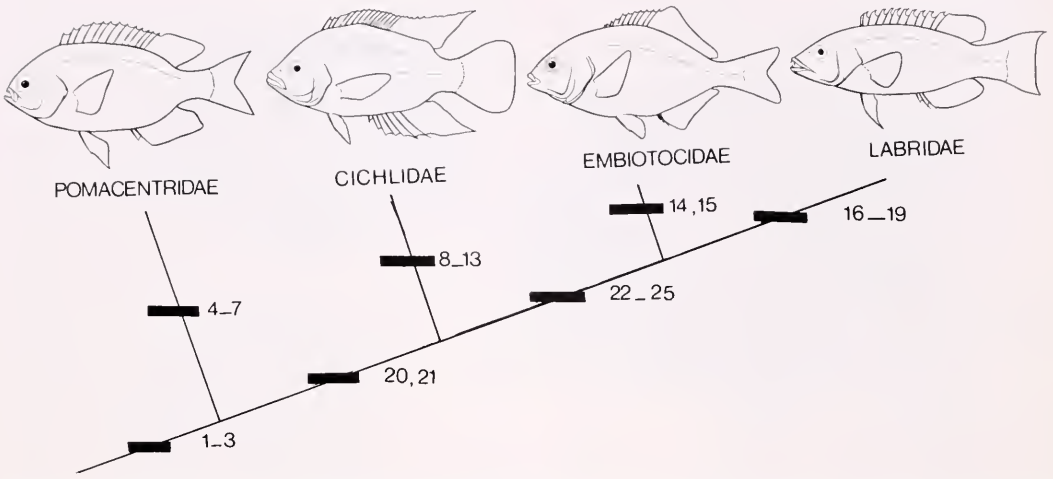


Figure 52. Interrelationships of the major labroid lineages based on the following specialized characters: **1,** United or fused fifth ceratobranchials; **2,** true diarthrosis between upper pharyngeal jaws and basicranium; **3,** undivided sphincter oesophagi muscle; **4,** strong sheet of connective tissue joining lower jaw with a ligament, which inserts on the ceratohyal bone; **5,** nipple-like bony process on ventral surface of lower pharyngeal jaw; **6,** pharyngo-cleithral articulation of characteristic form; **7,** obliquus posterior dominant muscle to lower pharyngeal jaw; levator externus 4 and obliquus posterior vertically aligned on fourth epibranchial, separated by oblique aponeurosis or tendon; **8,** transversus dorsalis muscle subdivided into four parts; **9,** premaxillae and maxillae functionally decoupled; **10,** cartilagenous cap on anterior border of epibranchial 2; **11,** microbranchiospinae of characteristic form present on outer faces of second, third, and fourth gill arches; **12,** A_2 and A_w portions of adductor mandibulae complex separated completely; insertion of large ventral division of A_2 onto angulo-articular; **13,** head of epibranchial 4 distinctly expanded; **14,** intra-uterine development of young with highly modified vascularized median fins; **15,** muscular sheet joining A_1 and $A_{2,3}$ portions of adductor mandibulae; **16,** levator posterior dominant muscle to the lower pharyngeal jaw, forming a force couple with the pharyngocleithralis muscle; **17,** toothplates of fourth pharyngobranchials absent or reduced; **18,** fourth epibranchials highly modified, articulating with upper pharyngeal jaws; **19,** true pharyngo-cleithral articulation functioning as sliding and hinge joint; **20,** levator externus 4 is a continuous muscle joining prootic region to muscular process on lower jaw; **21,** predisposition for insertion of levator posterior muscle on lower pharyngeal jaw; **22,** loss of second pharyngobranchial toothplates; **23,** first three branchial adductor muscles cover anterodorsal faces of the epibranchials; **24,** ligament connecting postmaxillary process of maxilla with anterior border of palatine and ectopterygoid; **25,** tooth rows arranged radially across the lower pharyngeal jaw, teeth located directly over the symphysis between left and right fifth ceratobranchials, dominant mode of tooth replacement from posterior margin of toothplate. (From Kaufman and Liem, 1982.)

functional separation of the lower pharyngeal jaw-parasphenoid bite from the swallowing mechanism. It is therefore possible that *Badis* is the primitive sister group of the Anabantoidei.

The Pomacentridae (damselfishes), Embiotocidae, and the Cichlidae have been considered members of the percoids for many years (Regan, 1913). We deviate from this traditional scheme and link the three families together with the Labridae, Odacidae, and Scaridae into one monophyletic assemblage (Fig. 52) at the subordinal rank: The Labroidei (also see Stiassny, 1981; Kaufman and Liem, 1982).

The Labroidei. The Labroidei are composed of the Pomacentridae (damselfishes), Cichlidae, Embiotocidae (surfperches), Labridae (wrasses), Odacidae, and Scaridae (parrotfishes). The Labroidei are characterized by (Stiassny, 1980; Kaufman and Liem, 1982): 1) united or fused fifth ceratobranchials resulting in the formation of one lower pharyngeal jaw, 2) a true diarthrosis between the upper pharyngeal jaws and the skull base without an intervening musculous part of the transversus dorsalis anterior muscle (Fig. 53), and 3) the presence of an undivided sphincter oesophagi muscle forming a continuous sheet (Fig. 53).

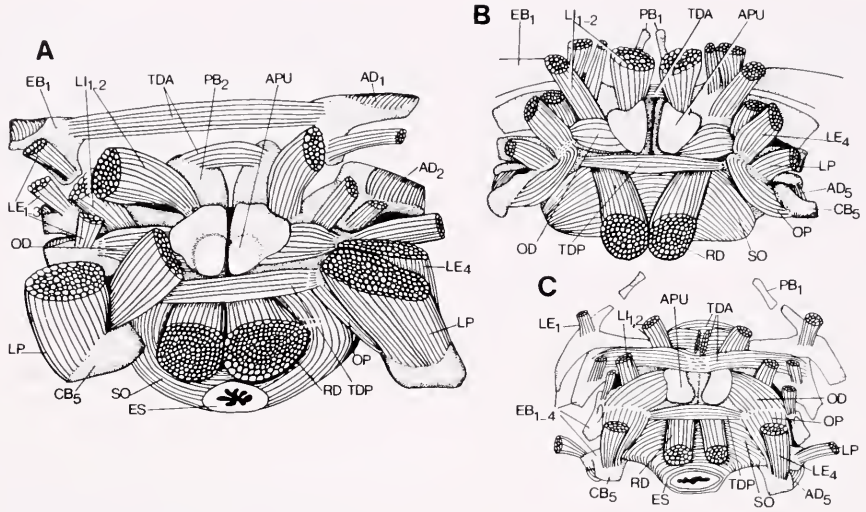


Figure 53. Dorsal aspect of the branchial musculature viewed from posterior to elucidate the muscles surrounding the esophagus and posterior branchial arches in representative Pomacentridae (A. *Tautogolabrus adspersus*. B. *Amphiprion xanthurus*); representative cichlid (C. "*Haplochromis*" *leuciscus*) (From Kaufman and Liem, 1982).

Abbreviations: AD, adductor branchialis; APU, apophysis of upper pharyngeal jaw (third pharyngobranchial); CB_5, fifth ceratobranchial (lower pharyngeal jaw, LPJ); EB, epibranchial; ES, esophagus; LE, levator externus muscle; LI, levator internus muscle; LP, levator posterior muscle; OD, obliquus dorsalis; OP, obliquus posterior muscle; PB, pharyngobranchial; RD, retractor dorsalis muscle; SO, sphincter oesophagi muscle; TDS, transversus dorsalis anterior muscle; TDP, transversus dorsalis posterior muscle.

The Pomacentridae is considered the primitive sister group of all other labroids (Stiassny, 1980). In pomacentrids the fourth levator externus and levator posterior muscles insert on the fourth epibranchials, a plesiomorphous condition found also in all primitive perciforms. Pomacentrids can be defined by 1) the presence of a strong connective tissue sheet connecting the medial face of the lower jaw via a cylindrical ligament with the ceratohyal (Stiassny, 1981); 2) a pair of nipplelike processes are present on the ventral surface of the lower pharyngeal jaw serving as insertion sites for the pharyngohyoideus muscle; 3) the muscular processes of the lower pharyngeal jaw abut the cleithra; and 4) the obliquus posterior muscle is prominent and is separated from the fourth levator externus by a distinct aponeurosis (Fig. 53). The fibers of the fourth levator externus and obliquus posterior muscles are not continuous. Pomacentrids are represented by about 23 genera with 230 species inhabiting all tropical seas, but primarily the Indo-Pacific.

The freshwater family Cichlidae has recently been defined (Liem and Greenwood, 1981; Stiassny, 1980, 1981; Kaufman and Liem 1982) by at least five shared derived characters: 1) the transversus dorsalis muscle is subdivided into four parts (Fig. 53); 2) microbranchiospinae of characteristic form are present on the gill arches; 3) the presence of an extensive cartilaginous cap on the anterior border of the second epibranchial (Fig. 54); 4) the A_2 and A_W portions of the adductor mandibulae complex are separate; and 5) the head of the fourth epibranchial is expanded. The Cichlidae comprise about 85 genera and well over 1,000 species. Cichlids are known for their complex territorial, agonistic and courtship behavior (Baerends and Baerends-van Roon, 1950; Wickler, 1962, 1963; Keenleyside, 1979), and the frequent occurrence of color and

trophic polymorphism (Fryer and Iles, 1972; Sage and Selander, 1975; Kornfield and Koehn, 1975). A spectacular evolutionary radiation occurs amongst the endemic cichlids inhabiting Lakes Victoria, Malawi and Tanganyika (Fryer and Iles, 1972; Greenwood, 1974). Speciation (Greenwood, 1974), morphological and functional diversification (Liem, 1978, 1979, 1980) and ecological dominance (Fryer and Iles, 1972; Liem, 1982) of the cichlids of Lakes Victoria, Malawi, and Tanganyika are considered accentuated if compared with similar phenomena in other vertebrates.

Phylogenetically, the Cichlidae represent the most primitive labroid in which the fourth levator externus becomes inserted on the lower pharyngeal jaw (Liem, 1974). Ontogenetically the fourth levator externus gains its attachment of the lower pharyngeal jaw by fusing with a large medial head of the obliquus posterior muscle (Aerts, 1982; Fig. 53). Thus the cichlid lower pharyngeal jaw is suspended in a muscular sling, part of which can be kept in continuous tension. Such a structural specialization facilitates the controlled protrusion, retrusion, and lateral translation, as well as rotation about three axes of the lower pharyngeal jaw (Liem, 1978). This specialized pharyngognathy of the cichlids is shared with the more derived Embiotocidae and Labridae (Fig. 52).

The Embiotocidae (surfperches) are coastal marine fishes (one species lives in freshwater), which are fully viviparous, delivering large well-developed young. The males have a small, intromittent organ, representing a modified forward end of the anal fin. Monophyly of the embiotocids can be established by the highly specialized viviparity and associated structural, physiological and behavioral features involving specialized and vascularized median fins (Webb and Brett, 1972). In respect to the jaw mechanisms, embiotocids share a specialized feature: a small slip of parallel muscle fibers arising from the anteromedial region of the part A_1 of the adductor mandibulae muscle and inserting upon the dorsal aponeurosis of part $A_{2,3}$ of this muscle complex (Stiassny, 1981).

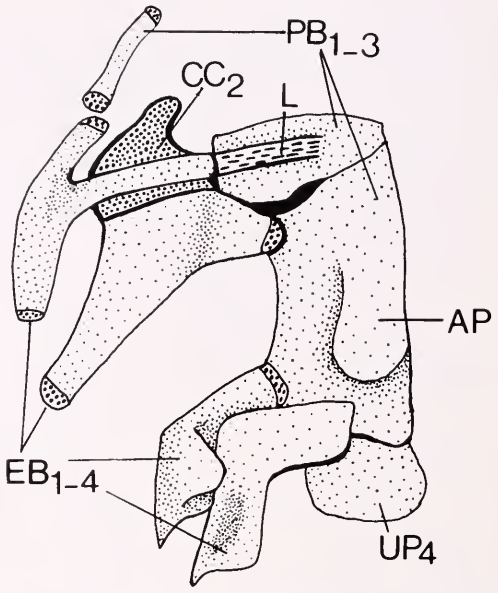


Figure 54. Dorsal view of dorsal gill arch elements of a representative member of the Cichlidae ("*Haplochromis*" *leuciscus*).

Abbreviations: AP, articular process of the upper pharyngeal jaw on the third pharyngobranchial; CC_2, cartilaginous cap on the 2nd epibranchial; EB_{1-4}, epibranchials 1–4; L, ligament; PB_{1-3}, pharyngobranchials 1–3; UP_4, upper toothplate of the fourth branchial arch.

The Labridae as defined by Kaufman and Liem (1982) include the wrasses (formerly known as the Labridae), Odacidae, and the parrotfishes (Scaridae). The inclusion of the odacids and scarids in the Labridae reflects the monophyletic nature of the assemblage and the recency of their common descent. The Labridae (including "odacids" and "scarids") can be defined as follows: 1) The levator posterior muscle is the dominant muscle of the lower pharyngeal jaw forming a force couple with the pharyngocleithralis externus muscle (Liem and Greenwood, 1981); 2) The toothplates of the fourth pharyngobranchials are absent (Nelson,

1967b; Stiassny, 1981); 3) The fourth epibranchials are highly modified and of a characteristic form; 4) The adductor branchialis muscles of all arches are hypertrophied (Fig. 53); and 5) There is some form of physical contact between the lower pharyngeal jaw and the cleithrum (pharyngocleithral joint of Liem and Greenwood, 1981). The labrids comprise over 70 genera and about 470 species, and play a key role in modern tropical marine communities. Many labrids cause patchy disturbances to sessile invertebrates (Kaufman and Liem, 1982) and represent a principal factor regulating food abundance for other reef organisms. The disproportionate role of labrids in determining the distribution and abundance of benthic organisms in tropical marine hard-bottom communities may be correlated with the specialized lower pharyngeal jaw (LPJ) which is functionally versatile in processing a broad range of prey.

In the phylogenetic scheme of the Labroidei (Fig. 52), the Embiotocidae and Labridae are considered sister groups on the basis of four synapomorphies: 1) The second pharyngobranchial toothplates are absent (G. Nelson, 1967b; Stiassny, 1981); 2) The first three branchial adductor muscles cover the anterodorsal surfaces of the epibranchials (Stiassny, 1980); 3) a ligament connects the postmaxillary process of the maxilla with the anterior border of the palatine and ectopterygoid (Stiassny, 1980); and 4) tooth rows are arranged radially across the LPJ, with teeth located directly over the symphysis between left and right fifth ceratobranchials.

Other Suborders. The Acanthuroidei, the marine surgeonfishes (Acanthuridae) and rabbitfishes (Siganidae), is often thought to form the link between the more generalized perciforms and the Tetraodontiformes. Although the relationship between acanthuroids and tetraodontiforms is often implied (Winterbottom, 1974b, Tyler, 1980), no synapomorphies have so far been found. Acanthuroids all have deeply compressed bodies, large swimbladders, and pass through a highly specialized planktonic acronurus larval stage. The mesethmoid bone is positioned well in front of the lateral ethmoids and is distinctly separated from the vomer by a forward extension of the parasphenoid (Starks, 1926). Many of the over 85 species of acanthuroids are herbivorous and feed on algae.

The Blennioidei, which includes 35 families, 245 genera, and over 900 species (Springer, 1968, 1972; Smith-Vaniz and Springer, 1971) is most likely a polyphyletic assemblage (Gosline, 1968). According to Bertin and Arambourg (1958) blennioids can be distinguished by the firm attachment of the fin rays of the pectoral fin to the hypertrophied pterygiophores. Blennioids have elongate bodies with long dorsal and anal fins, large pectoral fins and small pelvic fins placed far forward. Included among the blennioids are the sandfishes (Trichodontidae), jawfishes (Opisthognathidae), sandperches (Mugiloididae), sanddivers (Trichonotidae), venomous weeverfishes (Trachinidae), stargazers (Uranoscopidae) which have very venomous spines at the edge of the opercle and electric organs behind the eyes, sand stargazers (Dactyloscopidae), cod icefishes (Nototheniidae) from coastal antarctic waters living at an average temperature of $-1.9°$ C and using a glycoprotein in the blood as antifreeze (DeVries and Wohlschlag, 1969), crocodile icefishes (Chaenichthyidae) which lack hemoglobin in their blood, eelblennies (Congrogadidae), snake blennies (Ophiclinidae; Springer, 1970), threefin blennies (Tripterygiidae), clinids (Clinidae; Stephens, 1963; Springer, 1964), combtooth blennies (Blenniidae; Springer 1968, 1972; Springer and Smith-Vaniz 1972; Smith-Vaniz and Springer, 1971) comprising over 275 species, pricklebacks (Stichaeidae; Makushok, 1958), and wolf fishes (Anarhichadidae). Generally, blennioids are semisedentary bottom forms that live along rocky shores. But the sand-living species have special fea-

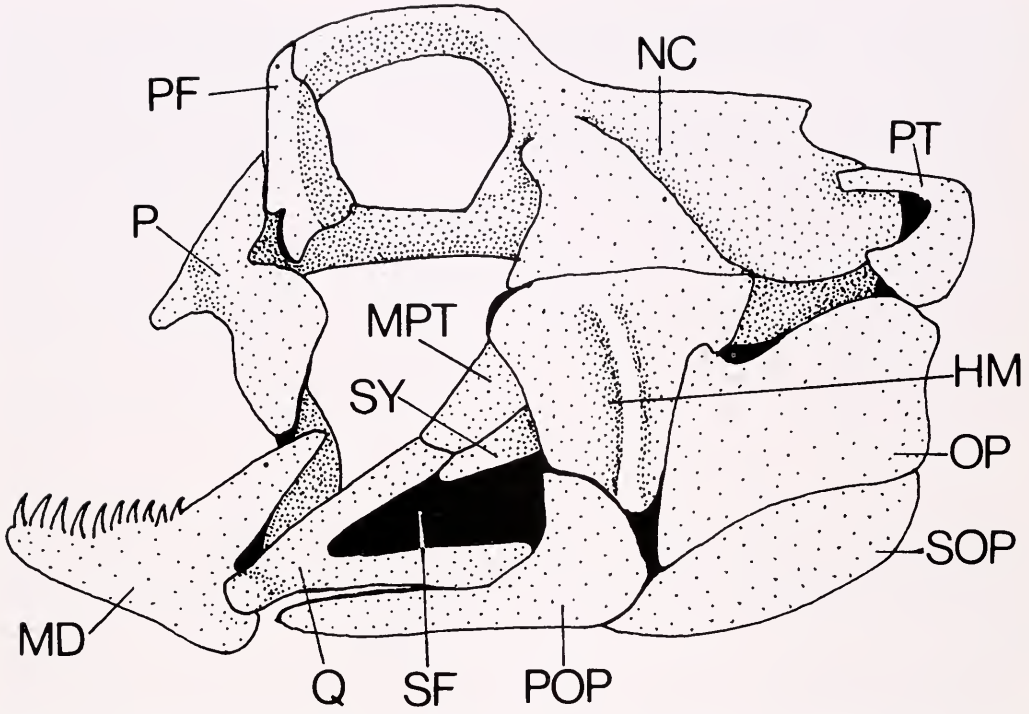


Figure 55. Lateral view of neurocranium, suspensorium, and opercular apparatus in a representative gobioid *Periophthalmus* (Modified from Gregory, 1933).

Abbreviations: SF, the large foramen in the suspensorium; HM, hyomandibula; MD, mandible; MPT, metapterygoid; NC, neurocranium; OP, operculum; P, palatine; PF, lateral ethmoid complex; POP, preoperculum; PT, posttemporal; Q, quadrate; SF, foramen in suspensorium; SOP, suboperculum; SY, symplectic.

tures such as eyes placed on the top of the head, and their upward-directed mouths have fringes, or flaplike structures thought to prevent the intake of sand with the respiratory current which is produced by a dominant opercular suction pump.

The Gobioidei is another extremely speciose suborder containing 7 families, 235 genera and over 1,000 species. Although monophyly is relatively well documented, internal classification is still chaotic (Gosline, 1968). Gobioids are characterized by the loss of the parietals, circumorbitals, the lateral line, and pyloric caeca. A very large space ("foramen") is located in the center of the suspensorium surrounded by the two arms of the quadrate bone, the symplectic and preoperculum giving the gobioid suspensorium a very characteristic structural pattern (Fig. 55). Among the gobioids (Bohlke and Robbins, 1960, 1968; Koumans, 1953) are the sleepers (Eleotridae), gobies (Gobiidae), which is the largest family of marine fishes forming together with blenniids and clinids the dominant element in the benthic habitat of tropical reefs, sand gobies (Kraemeriidae), eellike gobies (Gobioididae), burrowing gobies (Trypauchenidae), and wormfishes (Microdesmidae).

The marine Stromateoidei is unquestionably monophyletic since all members have very specialized toothed saccular outgrowths of the esophagus (Haedrich, 1967). Stromateoids comprise 6 families, 15 genera and about 60 species and in-

clude the medusafishes (Centrolophidae), driftfishes (Nomeidae), squaretails (Tetragonuridae), and butterfishes (Stromateidae).

The marine Scombroidei includes the world's fastest swimming fishes. Scombroids are specialized in many ways for high speed swimming (Gibbs and Collette, 1966; Fierstine and Walters, 1968). The single synapomorphy is the highly modified upper jaw: the premaxillae are not only united with each other but also with the maxillae, forming a rigid nonprotrusible upper jaw which can become elongate to form a rostrum. Scombroids comprise 6 families with 36 genera and over 90 species. Included are the snake mackerels (Gemphylidae), cutlassfishes (Trichiuridae), mackerels and tunas (Scombridae; Gibbs and Collette, 1966), swordfish (Xiphiidae), and billfishes (Istiophoridae) (Gregory and Conrad, 1937, 1943).

Smaller perciform suborders include the following: 1) The Kurtoidei, with a single genus. These forehead brooders possess hooks developed from the supraoccipital bone and have expanded ribs forming a bony tube enclosing the swimbladder; 2) The burrowing Ammodytoidei, the sand lances, with elongate bodies, protrusible premaxillae (Kayser, 1962), the lower jaw projecting forward beyond the upper jaw, and neither fin spines nor pelvic fins; 3) The Callionymoidei (Kayser, 1962), the dragonets, resemble the blennioid trichodontids in having a specialized pectoral fin skeleton in which the scapula is aligned together with the pterygiophores and functions as a direct articulation for the top three pectoral fin rays (Starks, 1923); 4) The elongate Mastacembeloidei, the spiny eels, with the dorsal fin preceded by a series of isolated spines and the supracleithrum attached to the second and third vertebra by a distinct ligament while the posttemporal is absent. The premaxillae are firmly united with the maxillae. Travers (personal communication) has proposed that the mastacembeloids are more closely related to the synbranchiforms than to any other teleost; 5) The Sphyraenoidei encompassing one family, the Sphyraenidae (barracudas; de Sylva, 1963), with elongate bodies and jutting jaws with strong fanglike teeth, and small gill rakers; 6) The Polynemoidei (threadfins) with a subterminal mouth; and 7) The Mugiloidei (mullets), in which the oral dentition is often reduced and the pharyngeal jaw apparatus and gill rakers are modified to form a filtering device.

The Anabantoidei comprise five families, 16 genera and about 70 species. All anabantoids have accessory air breathing organs and possess a dual respiratory strategy: aquatic and aerial, the proportions of each depending on the oxygen and carbon dioxide content of the water, and the pH and temperature of the water. Anabantoids, as defined here, represent a monophyletic assemblage (Fig. 56) containing the Anabantidae (climbing gouramies), Belontiidae (gouramis, bettas and paradise fishes), Helostomatidae (kissing gouramis), Osphronemidae (giant gouramis), and the Luciocephalidae (pikehead). Monophyly is based on the following shared derived characters. 1) The suprabranchial air chamber is clearly separated from the buccopharyngeal cavity, and respiratory air is confined to the suprabranchial cavity (Fig. 57; Liem, 1981). Communication between the buccopharynx and suprabranchial cavity (Fig. 58) is by means of a) a pharyngeal opening protected by a valve which is derived from modified gill rakers and/or b) a branchial opening located between the first and second arches. (In the Luciocephalidae the pharyngeal opening is absent and communication between suprabranchial cavity and buccopharynx is restricted to the branchial opening.) 2) The principal organ for aerial respiration is supported by an enlarged and modified first epibranchial bone. 3) All members have the swimbladder extending posteriorly as far as the parhypural. 4) A distinct foramen

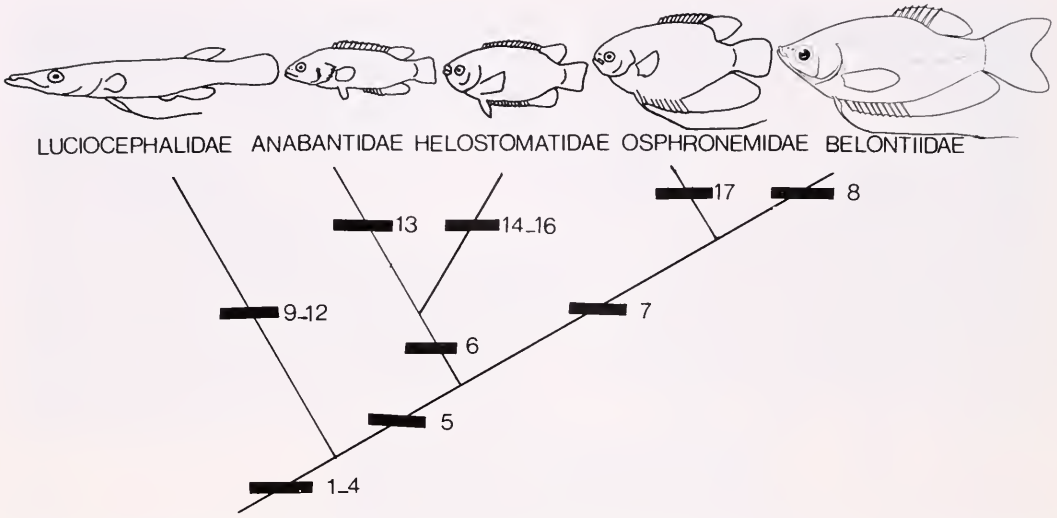


Figure 56. Interrelationships of the Anabantoidei based on the following specialized features: **1,** the suprabranchial air chamber is clearly separated from the buccopharyngeal cavity and respiratory air is confined to the suprabranchial cavity; **2,** principal organ for aerial respiration is supported by an enlarged and modified first epibranchial bone; **3,** swimbladder extends posteriorly into the tail as far as the parhypural (Liem, 1967a); **4,** a distinct foramen exoccipitale, covered by a tympanumlike membrane is present in the exoccipital bone; **5,** basioccipital with distinct pharyngeal processes (see Liem, 1963, Figs. 14–26, and 40–50); **6,** parasphenoid with very distinct transverse processes (Liem, 1963, Figs. 40–42, 44); **7,** parasphenoid with prominent, median ventrally directed pharyngeal process (Liem, 1963, Figs. 17, 19–93); **8,** loss of the ectopterygoid; **9,** median gular element present (Liem, 1967a); **10,** highly specialized premaxillae, lower jaw, and jaw protrusion mechanism (Lauder and Liem, 1981); **11,** dorsal and anal spines lost; **12,** no pharyngeal opening between the suprabranchial and buccopharyngeal cavities, and a specialized second adductor branchialis muscle running in the posterior margin of the floor of the suprabranchial cavity; **13,** fifth ceratobranchials are connected to each other to form a lower pharyngeal jaw, which bites against the toothed transverse process of the parasphenoid with the actions of the levatores posterior and externi muscles (Liem and Greenwood, 1981); **14,** the dentary rotates freely in the vertical plane around the articular; **15,** dentary and premaxillae are toothless; **16,** basibranchial with median, prominent, vertical, shelflike processes; **17,** a well-developed rostral fossa extending posteriorly nearly reaching the level of the posterior border of the orbit, formed by the ethmoid and frontals (Liem, 1963, Fig. 4).

exoccipitale, covered with a tympanumlike membrane overlying the sacculus, is present in the exoccipital bone (Liem, 1963, 1967), except in *Helostoma temmincki* and *Sandelia capensis*. Within the Anabantoidei we can recognize four major clades, each of which is defined by major specialized characters (Fig. 56). The Luciocephalidae (formerly classified as a separate order, e.g., Liem, 1963, or as a separate suborder, e.g., J. Nelson, 1976) represents a very specialized monotypic clade with numerous autapomorphic features (see Liem, 1967; Lauder and Liem, 1981; and Fig. 56). The Anabantidae, Helostomatidae, Osphronemidae, and Belontiidae possess distinct transverse processes of the basioccipital. The Belontiidae have lost the ectopterygoid bone. On the basis of the characters summarized in Figure 56, the Anabantidae and Helostomatidae are considered sister groups, and so are the Osphronemidae and Belontiidae. This new hypothesis of the interrelationships of the Anabantoidei differs significantly from that proposed by Liem in 1963. The predominant mode of air ventilation in Anabantoidei is quadruphasic (Peters, 1978; Liem, 1980): First, the fish rises to the surface and exhales all the air by flushing out the entire air bubble from the suprabranchial cavity into the oropharynx and out of the mouth (Fig. 58). This is accomplished by a coughing-like mechanism, which produces a reversed water current entering

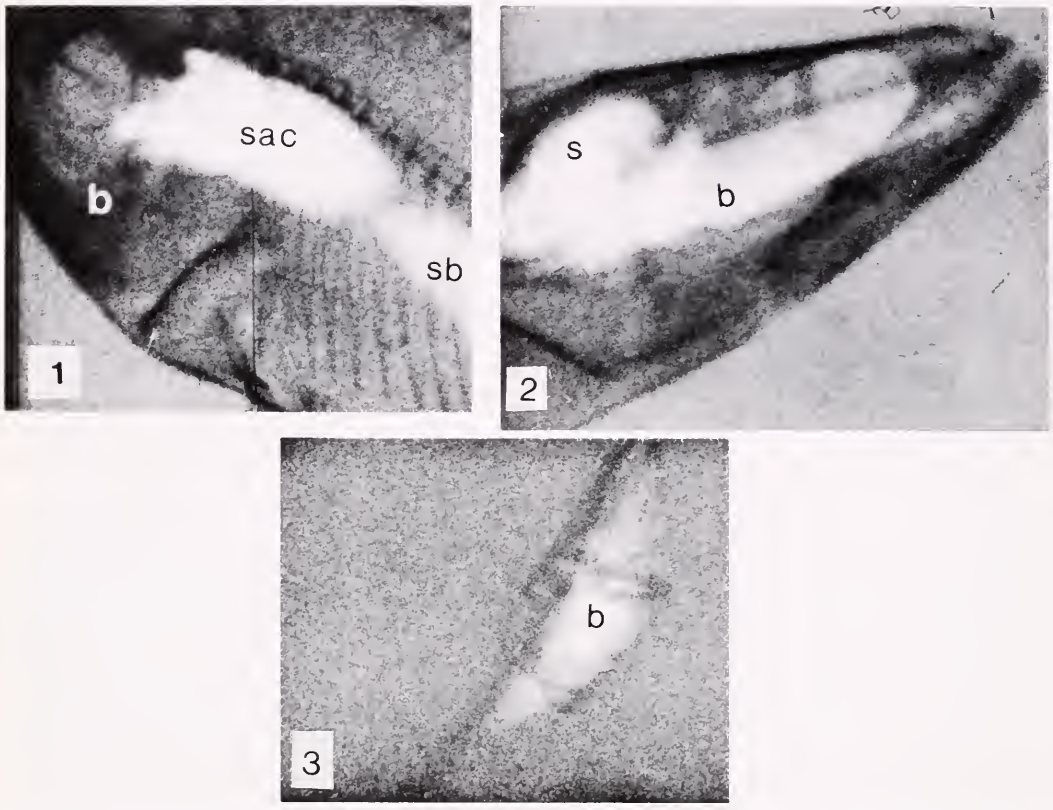


Figure 57. Prints of selected frames of x-ray film taken at 50 frames/sec. during the air breath in the anabantoid *Helostoma temmincki* (1), the channiform *Channa striatus* (2), and the synbranchiform *Monopterus albus* (3), to show where the respiratory air is stored in the live fish.

Abbreviations: b, buccopharyngeal cavity; s and sac, suprabranchial chamber; sb, gas bladder (swimbladder).

from underneath the gill cover into the suprabranchial cavity and then into the buccopharynx and out of the mouth. Exhalation is followed by inhalation during which air is compressed from the buccopharynx into the suprabranchial cavity via the pharyngeal and branchial openings. This pattern is found in all adult anabantoids except *Anabas*, which ventilates air triphasically: The fish rises to the surface and inhales air into the buccopharynx and compresses the air into the suprabranchial cavity (Liem, 1980). In this way "deoxygenated" air in the suprabranchial cavity escapes from underneath the gill cover and is replaced by fresh air (Liem, 1980; Peters, 1978). Adult *Helostoma* is capable of both quadruphasic and diphasic patterns of air ventilation. In most anabantoids the male builds foam nests and engages in parental care. According to our data and hypothesis, the Channiformes (Ophicephaliformes) is not closely related to the Anabantoidei (see p. 178).

The Scorpaeniformes

The order Scorpaeniformes containing 21 families, over 250 genera and about 1,000 species can be defined readily by two specializations: 1) In the skull a peculiar bony posterior extension of the third circumorbital (suborbital, infraor-

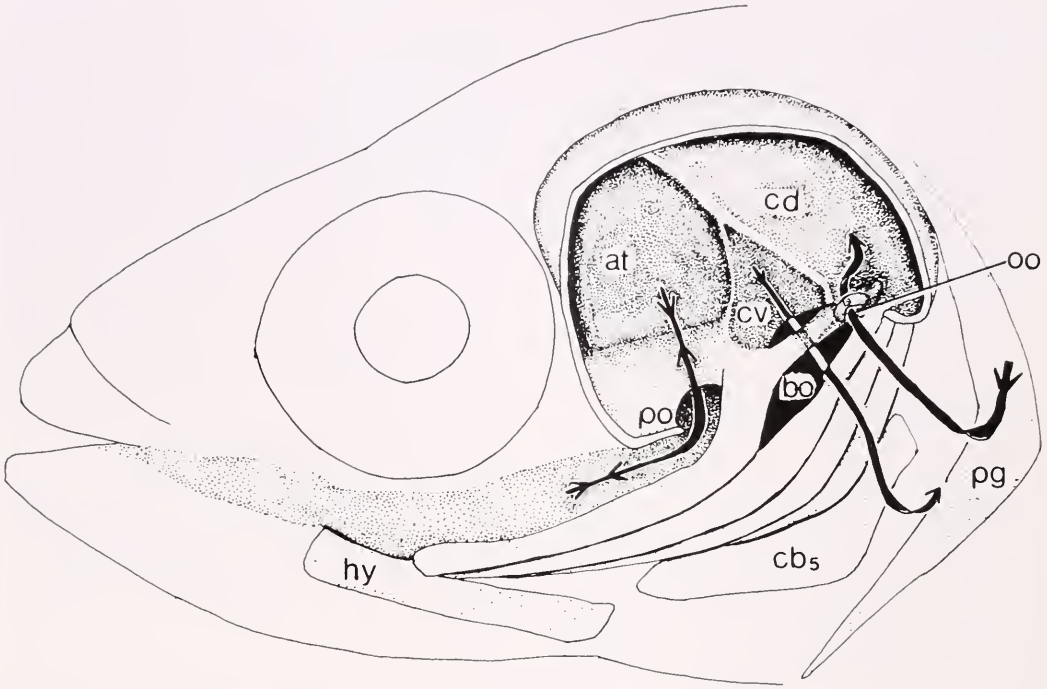


Figure 58. Lateral view of the suprabranchial cavity of a representative anabantoid fish after removal of the side of the head. Gills and "labyrinth organ" have been removed. Arrows indicate pathways for air and water. Structure over oo is a thickening of the operculum, shown here separately as a C-shaped sausagelike bulge. This bulge can be pressed tautly against the muscular process of the first epibranchial on which it lies, closing the opercular opening (oo). (From Liem [1980b], courtesy of Plenum Publishing Co.)

Abbreviations: at, atrium; bo, branchial opening; cb_5, fifth ceratobranchial; cd, caudodorsal compartment; cv, caudoventral compartment; hy, hyoid; oo, opercular opening; pg, pectoral girdle; po, pharyngeal opening in floor of the suprabranchial cavity.

bital) bone extends across the cheek to contact the outer surface of the preoperculum (Gutberlet, 1915; Rendahl, 1933); 2) In the caudal skeleton two platelike hypurals are sutured to the terminal half centrum. In general the scorpaeniform head and body tend to be spiny or bony-plated as a result of hypertrophied or otherwise specialized integumentary ossifications. The phylogenetic relationships of the scorpaeniforms are unknown (Fig. 50) and the internal classification is still chaotic (Quast, 1965). Provisionally, we subdivide the scorpaeniforms into four suborders. The Scorpaenoidei, which remains ill defined, containing among others, the Scorpaenidae (rockfishes; Eschmeyer, 1965, 1969; Eschmeyer and Collette, 1966) with venom glands in the dorsal, anal, and pelvic spines and with internal fertilization as the dominant reproductive mode. The family contains about 60 genera with 330 species. The live-bearing genus *Sebastes* is the largest family with about 100 species. The Synanceiidae (stonefishes), has venom glands near the base of hypodermiclike dorsal fin spines and the neurotoxin of stonefishes is the most deadly of fish venoms (Halstead, 1970). The Triglidae (sea robins), have the lower two or three pectoral rays independent and greatly elongated. The Hexagrammoidei (greenlings and sablefishes), is a poorly defined taxon and greenlings constitute the richest family endemic to the North Pacific. The Platy-

cephaloidei (flatheads; Matsubara and Ochiai, 1955) have a very depressed head. The Hoplichthyidae (ghost flatheads) and Congiopodoidei (pigfishes) represent two small suborders of unknown phyletic status. The Cottoidei, which can be characterized by the loss of the basisphenoid bone, contain, among others, the Cottidae (sculpins, Bolin, 1947; Watanabe, 1960) with over 65 genera with about 300 species, Agonidae (poachers), and Cyclopteridae (lumpfishes and snailfishes).

Channiformes (Ophiocephaliformes) and Synbranchiformes

We will discuss the Channiformes (snakeheads) in conjunction with the Synbranchiformes (swamp eels, rice eels), in order to emphasize our hypothesis that the two orders are closely related to each other. Travers (personal communication) has put forward a hypothesis in which the Mastacembeloidei are included in the Synbranchiformes. In most previous classifications the Channiformes is considered to be closely related to the Anabantoidei on the basis of the presence of a modified first epibranchial as a support for the accessory air breathing organ. Here we will present data refuting the hypothesis that the Channiformes is a sister group of the Anabantoidei and formulate a competing hypothesis that the Channiformes are closely related to the Synbranchiformes. First we will define the Channiformes and Synbranchiformes and then discuss the relationships of the two groups.

The Channiformes. This assemblage contains only one genus *Channa (Ophicephalus, Ophiocephalus*; Myers and Shapovalov, 1931). All species are relatively large predaceous fishes (15 cm–1.2 m) with elongate bodies, long dorsal and anal fins and no fin spines. They are capable of breathing air. Because many inaccuracies concerning the cranial osteology continue to be repeated in recent literature, we present several illustrations of the skull (Fig. 59) in order to define the Channiformes more accurately. Contrary to previous accounts (Day, 1914; Bhimachar, 1932; Gregory, 1933; Liem, 1963), the frontals of channiforms do not articulate with the parasphenoid (Fig. 59) and the metapterygoid (Fig. 59) does not articulate with the frontal and sphenotic. The channiforms can be defined by the following apomorphies: 1) The otic bulla for the sacculith is mostly contained in the prootic bone (Fig. 59). 2) The metapterygoid has an anterodorsally directed prominent uncinate process which approaches the neurocranium. It seems that the presence of this uncinate process of the metapterygoid has led to the misconception that an articulation between the palatoquadrate and neurocranium exists. Actually the process serves as an attachment of a strong, flat tendon of the massive levator arcus palatini muscle. The process is more prominent in larger specimens but does not achieve physical contact with the neurocranium. 3) Two ventral aortae emerge separately from the bulbus arteriosus (Ishimatsu *et al.*, 1979). The anterior ventral aorta supplies the first and second branchial arches, while the posterior ventral aorta gives rise to the third and fourth branchial arches, which are associated with the systemic circulation. 4) The accessory air breathing organs are the buccopharyngeal epithelium, the lining of the suprabranchial cavity, and the respiratory nodules on the first and second epibranchials, the hyomandibula and parasphenoid. The suprabranchial cavity is in open communication with the buccopharyngeal cavity (Liem, 1980b). Consequently air is present in both the buccopharyngeal and suprabranchial cavities (Fig. 57). 5) The first epibranchial is a greatly expanded plate, which is not folded, and is suspended by a very small first pharyngobranchial bone (Fig. 59).

The Synbranchiformes. The synbranchiformes (swampeels) comprise one family, the Synbranchidae, composed of

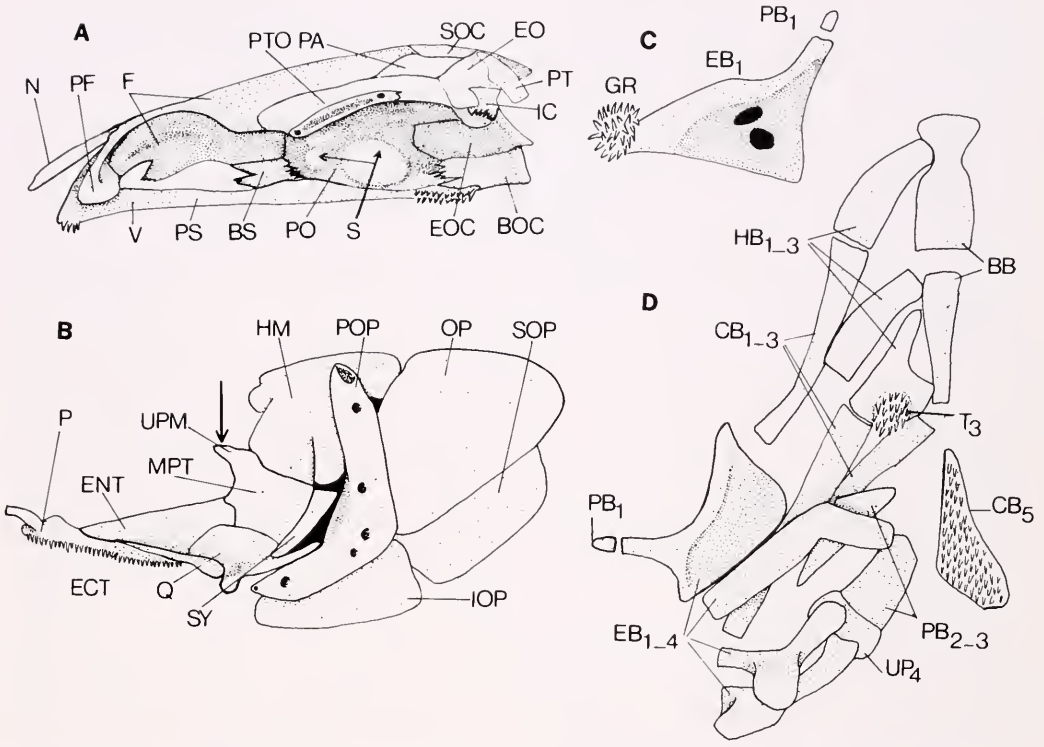


Figure 59. Osteology of the skull of a representative Channiform, *Channa striatus*. A. Lateral view of the neurocranium. B. Lateral view of suspensory and opercular apparatus. C. Ventrolateral view of first epibranchial bone. D. dorsal view of gill arches.

Abbreviations: BB, basibranchial; BOC, basioccipital; bs, basisphenoid; CB_5, fifth ceratobranchial; EB_{1-4}, epibranchials 1–4; ECT, ectopterygoid; ENT, entopterygoid; EO, epiotic; EOC, exoccipital; F, frontal; GR, gill raker on first epibranchial bone; HB_{1-3}, hypobranchials 1–3; HM, hyomandibula; IC, intercalary; IOP, interoperculum; MPT, metapterygoid; N, nasal; OP, operculum; P, palatine; PA, parietal; PB_{1-3}, pharyngobranchials 1–3; PF, lateral ethmoid complex; PO, prootic; POP, preoperculum; PS, parasphenoid; PT, posttemporal; PTO, pterotic; Q, quadrate; S, otic bullae; SOC, supraoccipital; SOP, suboperculum; SY, symplectic; T_3, toothplate on third hypobranchial; UP_4, upper toothplate of fourth branchial arch; UPM, uncinate process of metapterygoid; V, vomer.

4 genera (*Macrotrema*, *Ophisternon*, *Synbranchus* and *Monopterus*) with 15 species (Rosen and Greenwood, 1976). Travers (personal communication) includes the Mastacembeloidei within this order. This very specialized assemblage is unquestionably monophyletic and shares the following specializations: Eel-shaped fishes without pectoral fins in the adults, no pelvic fins or girdles and dorsal or anal fins. The gill membranes are united and continuous around the isthmus. In the uniquely specialized neurocranium the frontal bones are turned down and sutured to the basisphenoid (Rosen and Greenwood, 1976) and the large parietals meet in the midline. Synbranchiforms are the only teleosts with the suspensorium (palatoquadrate) articulating with a prominence on the basisphenoid, frontal or both, and with the vomer and lateral ethmoids, making the jaw suspension "amphistylic." The anterior and posterior nares are separated by a long distance, and are associated with an elongate nasal sac containing a highly developed nasal rosette. The circulatory system is remarkably specialized (Liem,

1961; Rosen and Greenwood, 1976) with a complete fourth aortic arch, which has important functional implications. Most synbranchiforms are protogynous hermaphrodites (Liem, 1968), are amphibious (Liem, 1967; Johansen, 1966), and have uniquely modified urinary bladders, which may function in the reabsorption of water when the fish is on land (Liem, in preparation). The larvae of some synbranchiforms have a special vascular specialization and large pectoral fins to exploit the oxygen-rich surface layer by creating an effective counter current of the blood stream and the respiratory current to maximize gas exchange (Liem, 1981). Thus the synbranchiforms are among the most specialized teleosts known in terms of skull structure, respiratory and vascular design, reproduction, development, and ecology.

Synbranchiform-Channiform Relationships. We offer a hypothesis that the Synbranchiformes and Channiformes are closely related to each other. Sister group relationships of the channiforms and synbranchiforms (excluding the Alabetidae or Cheilobranchidae, which are Gobiesociformes, p. 156) are based on the following synapomorphies. 1) The brain is elongate and the forebrain is characteristically modified by a fusion of the left and right hemispheres in the posterior half (van der Horst, 1918). The fusion occurs at the level where the sulcus ypsilanti stops. Anterior to this point a deep fissure between left and right hemispheres is present. The extensive cross-connection (commissure) of the posterior halves of the left and right hemispheres of the forebrain (Fig. 60) is a highly specialized feature occurring only in the channiforms and synbranchiforms among teleosts (van der Horst, 1918). In outgroups the left and right hemispheres of the forebrain are separated. In general, the brains of channiforms and synbranchiforms resemble each other very closely, except that the optic lobes of the channiforms are much larger than those of the synbranchiforms (Fig. 60). Such a difference can be correlated with the fact that channiforms are large-eyed visual fishes, while synbranchiforms have drastically reduced vision. 2) The adductor mandibulae complex is specialized in several ways. The entire complex is hypertrophied (Fig. 61). In synbranchiforms the adductor mandibulae part A_1 is no longer inserted on the maxilla and, instead, is attached to the mandible (Van Conner, 1966; Liem, 1980c). However, in the most primitive synbranchiform, *Macrotrema caligans*, the adductor mandibulae part A_1 is still inserted on the maxilla by means of a tendon on the lateral surface of the maxilla, in the middle of the ramus, as is the case in all channiforms. Such an insertion of A_1 on the ramus way below the maxillary head and halfway along the shaft of the bone is a specialization shared with all channiforms (Fig. 61). It is hypothesized that in advanced synbranchiforms the insertion of the maxilla is lost. In channiforms, the A_1 is also associated with a muscle that inserts on the mandible (Fig. 61). The channiforms and synbranchiforms also share a specialization of the adductor mandibulae part A_2, which occupies the most anterior position just behind the orbit, and completely overlies other muscles (Fig. 61). In both groups, the fiber direction, topography, hypertrophy, and insertion of A_2 on the ascending process of the dentary are identical. Further evidence that the synbranchiforms and channiforms are sister groups is the forward position of the orbits and the modified fourth aortic arch. In channiforms and the primitive *Macrotrema* the fourth aortic arch is composed of functionally almost continuous afferent and efferent branchial arteries which are connected by arterial loops (Ishimatsu *et al.*, 1979). In advanced synbranchiforms the fourth aortic arch is structurally and functionally one continuous vessel responsible for the systemic circulation. Both the Channiformes and Synbranchiformes (except for *Macrotrema*) use the bucco-

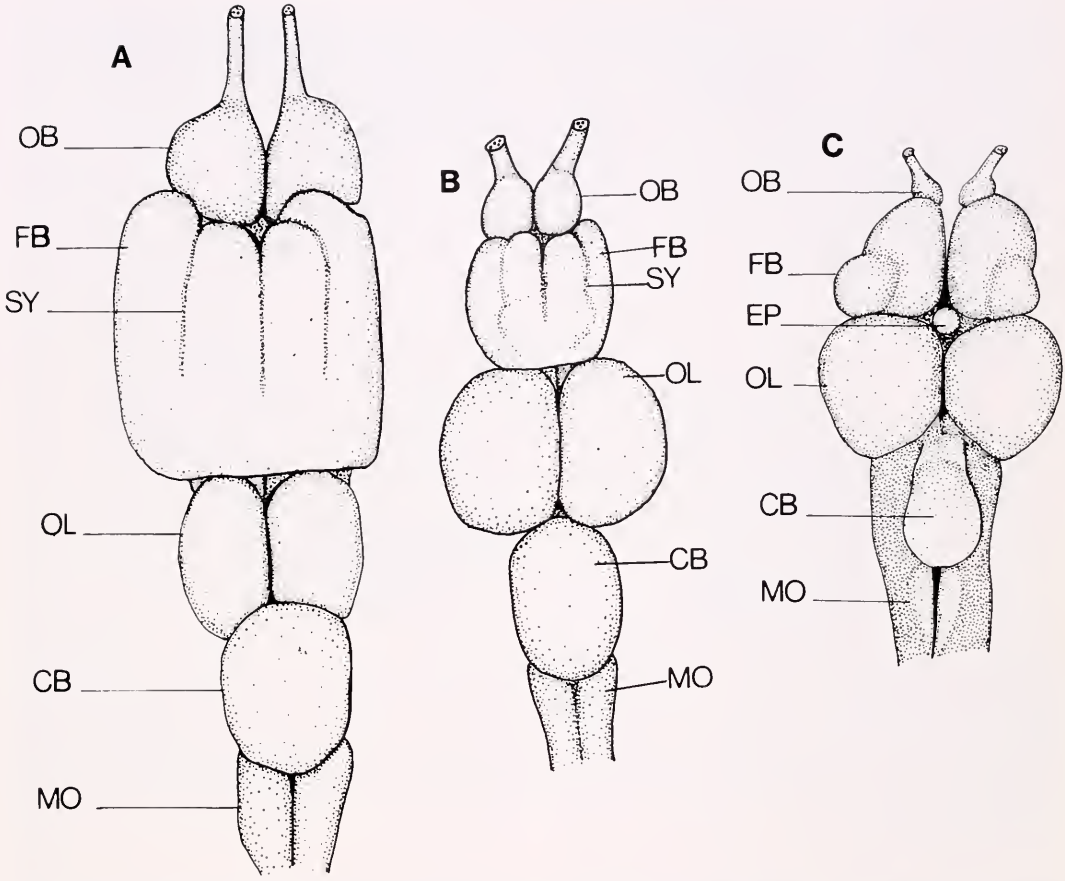


Figure 60. Dorsal views of the brains of: A. a primitive synbranchiform *Macrotrema caligans*. B. the channiform *Channa striatus*. C. the gobiesociform *Alabes dorsalis*. In A and B the forebrains are specialized in having the left and right halves coalesced posteriorly, while in C the primitive state of completely separated forebrain hemispheres is represented.

Abbreviations: CB, cerebellum; EP, epiphysis; FB, forebrain; MO, medulla oblongata; OB, olfactory bulbs; OL, optic lobes; SY, sulcus ypsilanti.

pharyngeal epithelium and the linings of outpocketings of the buccopharynx (e.g., *Monopterus cuchia*, all channiforms) for gas exchange with atmospheric air. These outpocketings maintain a continuously open communication with the buccopharynx.

Both groups have enlarged mesopterygoids (or entopterygoids). In channiforms (Fig. 59) the large mesopterygoid is very closely associated with the large toothed palatine and the small toothless ectopterygoid. Rosen and Greenwood (1976: 45–48) imply that the mesopterygoid in synbranchiforms is missing and that the ectopterygoid is large and toothed. Such an interpretation seems unlikely, if synbranchiforms and channiforms are sister groups. The topographical features of the bone in the synbranchiforms and the condition of the element in the channiforms indicate that the bone in synbranchiforms is an enlarged mesopterygoid (as in channiforms). The ectopterygoid is present as a small toothless element (Fig. 59). The olfactory rosette

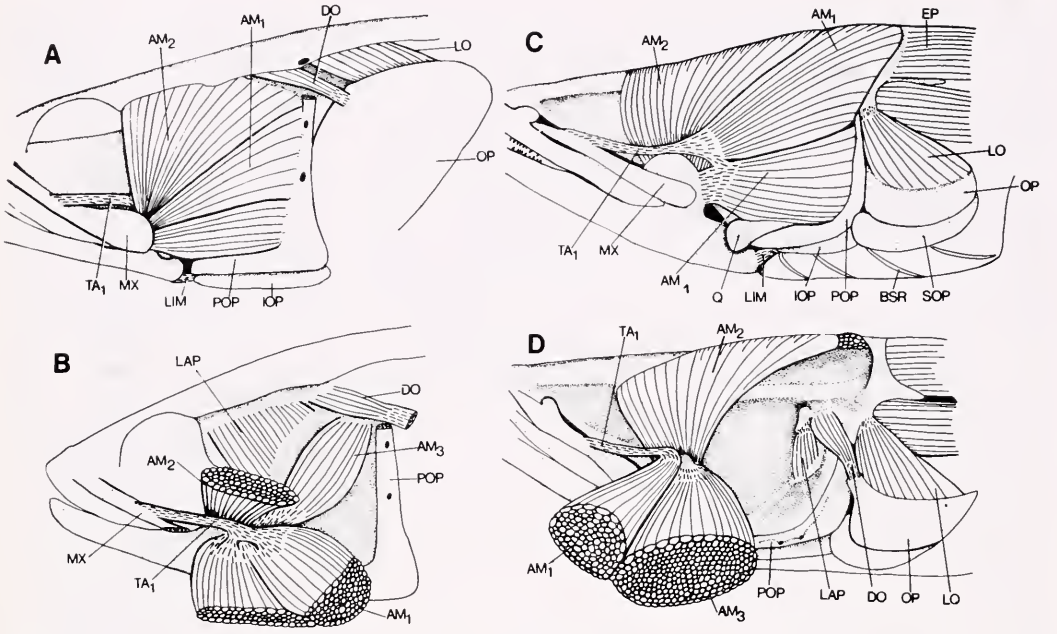


Figure 61. Lateral view of the main jaw musculature in: A and B, a representative channiform (*Channa striatus*); C and D, a primitive synbranchiform (*Macrotrema caligans*). A and C show the superficial musculature; B and D depict the deep jaw musculature.

Abbreviations: AM_1, part A1 of the adductor mandibulae complex; AM_2, part A2 of the adductor mandibulae complex; AM_3, part A3 of the adductor mandibulae complex; BSR, branchiostegal ray; DO, dilator operculi; EP, epaxial muscle; IOP, interoperculum; LAP, levator arcus palatini; LIM, interoperculomandibular ligament; LO, levator operculi; MX, maxilla; OP, operculum; POP, preoperculum; Q, quadrate; SOP, subopercular; TA, tendon of part A_1 of the adductor mandibulae complex.

in both groups is enlarged and has undergone complex elaborations.

The synbranchiforms differ from the channiforms in several important ways: Synbranchiforms have a greatly reduced levator arcus palatini muscle, which is hypertrophied in channiforms (Fig. 61). Synbranchiforms have an ossified interarcual cartilage while channiforms lack such an ossification, but have an expanded first epibranchial bone (Fig. 59). The heart of channiforms is located near the gill arches and shows a generalized structural configuration, while in synbranchiforms the heart is located far posteriorly (Liem, 1961), and its structural configuration deviates significantly from that of other teleosts. Finally, channiforms have a large swimbladder with a distinct caudal extension, while a swimbladder is lacking in synbranchiforms.

The channiforms are traditionally aligned with the anabantoids rather than with the synbranchiforms. Based on the above-mentioned synapomorphies, we hypothesize that channiforms may represent the plesiomorphic sister group of the synbranchiforms. With the available evidence we have not been able to establish sister group relationships of the channiforms with the anabantoids. Recently, Travers (1981) has described the presence of an ossified interarcual cartilage in the Carapidae, raising the question of possible synbranchiform-carapid relationships. However, the forebrain, the heart and aortic arches, the adductor mandibulae complex, and the urogenital

anatomy of the Carapidae are all in their primitive state. Thus, carapid-synbranchid relationships have not been established.

The Tetraodontiformes

This order dates back to the lower Eocene and is also known as the Plectognathi. It comprises about 320 species of mostly shallow water, circumtropical, and subtropical marine forms (Tyler, 1980). Tetraodontiforms are morphologically much more diversified than the great majority of fish groups of a comparable number of species. They range from 22 mm and 30 g to 2 m and 1,000 kg, from relatively normal shapes to strangely specialized forms with long tubular snouts and aborted caudal regions, from scaleless to heavily armored. Because tetraodontiforms show striking examples of extreme reductive evolution and represent one of the major end lines of the teleost radiation, the group is of considerable biological interest.

The tetraodontiforms are thought to represent a monophyletic assemblage based on the following characters (Tyler, 1980; Fig. 62). 1) The entire branchiostegal region is covered by a thick layer of scaleless or scaled skin, 2) The gill opening is greatly restricted and does not extend far below the base of the pectoral fin, 3) All members have lost the suborbital (circumorbital) bones, parietals, nasals, sensory canals in the skull bones, and anal fin spines.

Unfortunately the primitive sister group of the Tetraodontiformes remains unknown, although preliminary observations (Patterson, 1964; Tyler, 1968) indicate that it is the Acanthuroidei among the Perciformes. The Balistidae, Acanthuroidei and the berciform Pharmacichthyidae (Patterson, 1964) share a much elongate preorbital region of the neurocranium (as long as the lengths of the orbit and postorbital neurocranium combined), a ventrally bent parasphenoid in front of the orbit, a very small mouth, a long, strongly inclined suspensorium, and a very long and slender pelvic girdle, which ends between the much expanded coracoids. Actually it has been suggested (Patterson, 1964) that because adult balistids resemble larval acanthuroids, they may have been derived from acanthuroids by paedomorphosis. The phylogenetic scheme of the Tetraodontiformes presented here (Fig. 62) is tentative (Winterbottom, 1974b; Tyler, 1980) and awaits corroboration by the combined studies of R. Winterbottom and J. C. Tyler now in progress.

The Triacanthodidae (spikefishes) and Triacanthidae (triplespines) are considered sister groups of the lineage called Sclerodermi. The pelvis has large pelvic spines which can be locked, and the following pelvic muscles are hypertrophied: arrector dorsalis pelvicus, arrector ventralis pelvicus, and adductor superficialis pelvicus. The remaining six families share the single levator operculi and a distinct medial subdivision of the sternohyoideus muscle.

The Balistidae (triggerfishes and filefishes) and Ostraciidae (Ostraciontidae; boxfishes, trunkfishes and cowfishes) represent sister groups sharing the following specializations: The development of a deep A_1 subdivision of the adductor mandibulae complex, and the presence of a distinct retractor arcus palatini muscle (Winterbottom, 1974b). Some trunkfish produce ostracitoxin, which will kill other fishes in confined quarters.

The Triodontidae (three-toothed puffer), the lineage representing the Tetraodontidae (puffers) and Diodontidae (porcupine fishes), and the Molidae (molas) are tentatively represented by an unresolved trichotomy. All share the following specializations: 1) The loss of the intermandibularis and sternobranchialis muscles; 2) The A_1 part of the adductor mandibulae complex acquires an attachment to the prefrontal region of the skull; and 3) the A_2 part of the adductor man-

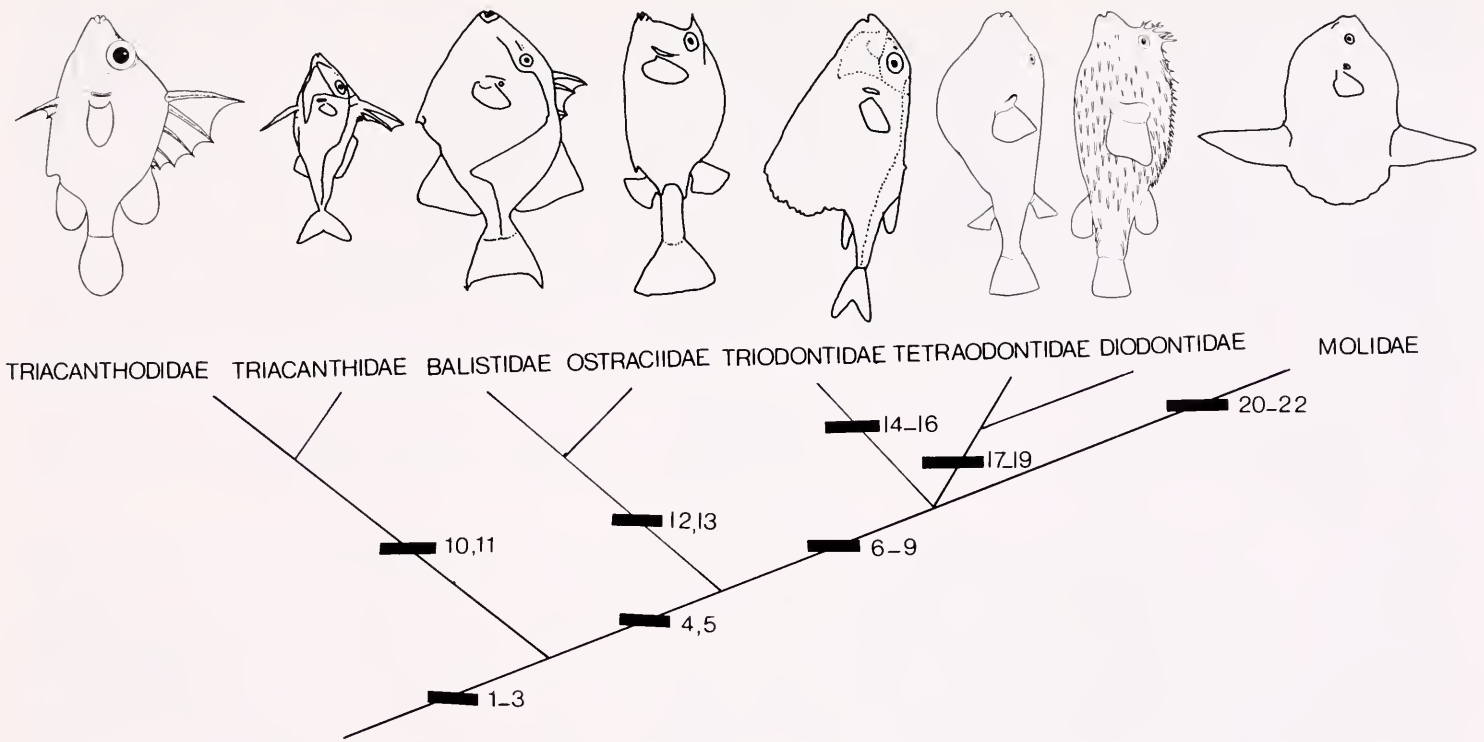


Figure 62. Interrelationships of the tetraodontiform fishes on the basis of the following specialized features: **1,** the entire branchiostegal region is covered by a thick layer of skin; **2,** the greatly restricted gill opening does not extend far below the base of the pectoral fin; **3,** suborbital bones, parietals, nasals, sensory canals in the skull bones and anal fin spines are absent; **4,** only a single levator operculi is present; **5,** a distinct medial subdivision of the sternohyoideus is present; **6,** the intermandibularis and sternobranchialis muscles are lost; **7,** A_1 muscle acquires an attachment to the prefrontal region of the skull; **8,** A_2 muscle is expanded dorsally and medially above A_3 to include the parasphenoid and prootic as the sites of origin; **9,** teeth are either small rounded units or long rodlike structures; **10,** pelvis with large pelvic spines, which can be locked in position; **11,** hypertrophy of the arrector dorsalis pelvicus, arrector ventralis pelvicus, and adductor superficialis pelvicus muscles; **12,** a distinct retractor arcus palatini muscle is present; **13,** differentiation of a deep A_1 muscle in the adductor mandibulae complex; **14,** cleithrum greatly elongate reaching forward underneath the lower jaw; **15,** a huge expansible dewlap of skin is present between the end of the pelvis and anus; **16,** presence in the spiny dorsal fin of one or two small spines borne on two basal pterygiophores; **17,** an inflatable diverticulum of the gut is present; **18,** fourth gill arch is lost and there is no gill slit between it and the fifth arch; **19,** muscle fibers from the dilatator operculi insert on the interoperculum, preoperculum and suboperculum; **20,** only a single ovary is present; **21,** otoliths are presumably lost; **22,** caudal region with numerous structural and functional specializations creating a unique mode of locomotion.

dibulae complex is expanded dorsally and medially above A_3 to include the parasphenoid and prootic as sites of origin. Each lineage of the unresolved trichotomy can be defined by synapomorphies (Fig. 62).

The Pleuronectiformes

The flat fishes represent a very specialized assemblage dating back to the Eocene. Pleuronectiformes (Heterosomata) contain 6 families, over 500 species and approximately 115 genera (Norman, 1934; Hubbs, 1945; Amaoka, 1969). All flatfishes are benthic and carnivorous.

The coherence of the pleuronectiforms as a monophyletic entity is based on the asymmetrical position of the eye. The condition wherein both eyes are on the same side of the head is clearly a derived one relative to all other vertebrates (Chabanaud, 1936, 1938). However, the position of the pleuronectiforms in relation to other major fish groups and the phylogenetic relationships within the order are still problematic.

Here we offer a tentative phylogenetic hypothesis of the Pleuronectiformes (Fig. 63). We recognize eight families, even though their delineation is often unclear. The most primitive family is the Psettodidae, with one genus *Psettodus* and two species, which retain the primitive character of the dorsal fin not extending onto the head (Fig. 63). No specialized characters set this family aside from the other seven.

All other seven families share the specialization of the loss of the following structures: palatine teeth, basihyal teeth, dorsal fin spines, and anal fin spines; the dorsal fin extends onto the head (Fig. 63). Among this lineage, the Citharidae (citharids; Hubbs, 1945) is the most primitive member and can be distinguished by the fact that the anus is deflected onto the eyed side. In the remaining six families the pelvic spines are lost (Fig. 63). Of the pelvic spineless members the Scophthalmidae may be the plesiomorphous group since the other five families are further specialized by the loss of vomerine teeth and having the branchiostegal membranes fused to one another rather than overlapping. The relationships between the Pleuronectidae (righteyed flounders; Norman, 1934) and the Bothidae (lefteyed flounders; Chabanaud, 1940) are still uncertain. The Rhombosoleidae shares the loss of a postcleithrum with the Soleidae and Cynoglossidae (Fig. 63), which are considered the most specialized members of the Pleuronectiformes. The Soleidae (soles) and Cynoglossidae (tonguefishes, tongue soles; Menon, 1977) are considered sister groups since both groups have lost their ribs and have the gill covers bound to one another across the throat by a thick layer of tough skin, which covers both the gill covers and the throat in between. Cynoglossids (Chabanaud, 1940) have pectoral fins without rays, becoming either unsupported membranous structures or lost altogether.

The phylogenetic interrelationships as hypothesized here are still problematic since they are based mostly on reductive characters. It is clear that further studies are needed to determine the phyletic relationships of the members of the Pleuronectiformes with greater confidence.

CONCLUSIONS

In this paper we have attempted to summarize current knowledge of the interrelationships of the ray-finned fishes. After more than a century of intensive study many of the major actinopterygian taxa remain poorly delimited and several cannot be defined by any uniquely derived characters (e.g., the Percomorpha). In providing a critical review of certain key aspects of actinopterygian evolution we have sought also to point out those areas where future research is badly needed. Above all, we consider that characters and their distributions must be the focus of a research program in actinopterygian phylogeny if progress is to be made. Theories of ancestry and descent,

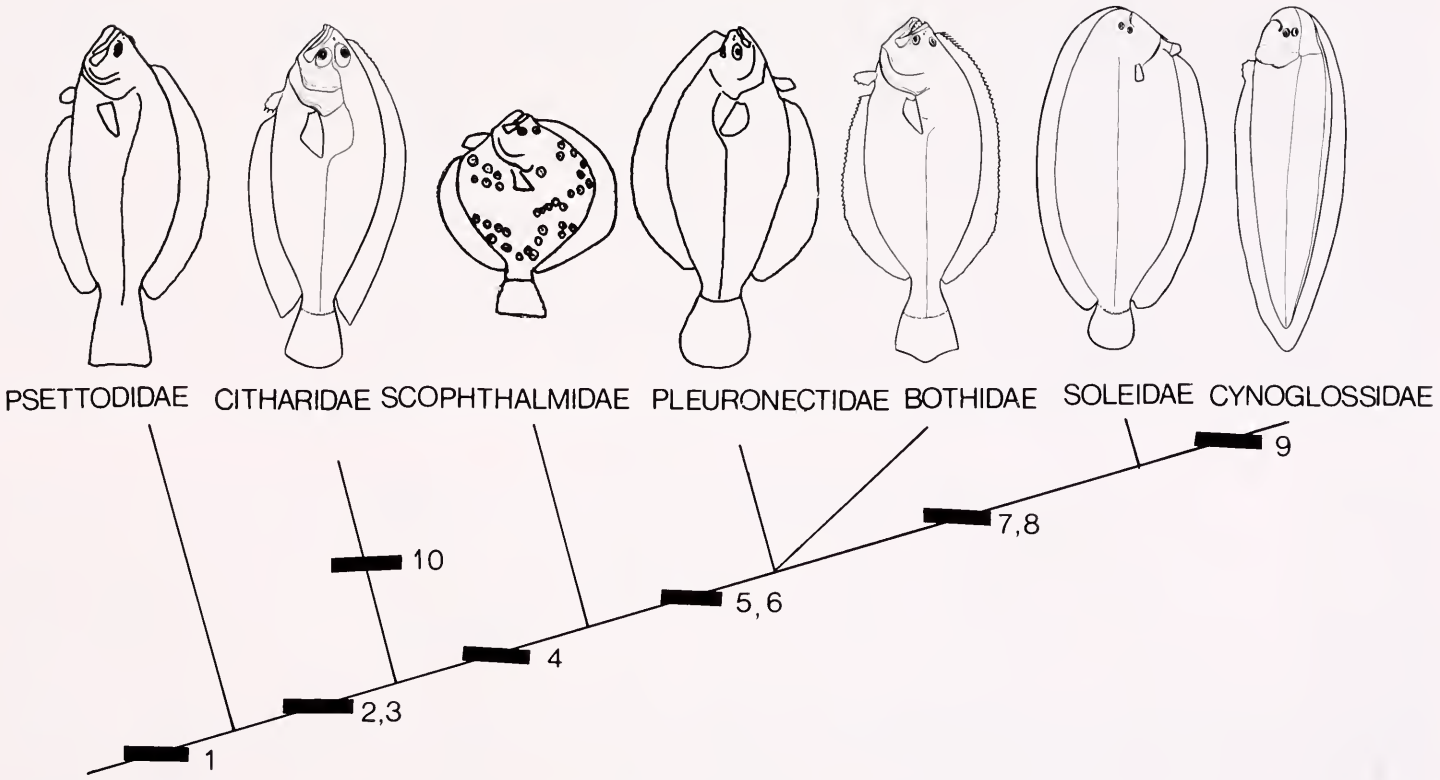


Figure 63. Interrelationships of the major lineages of the flatfishes (Pleuronectiformes) based on the following specialized characters: **1,** both eyes on the same side of the head; **2** loss of palatine teeth, basihyal teeth, dorsal spines and anal fin; **3,** dorsal fin extends onto the head; **4,** the spines of the pelvic fin are lost; **5,** vomerine teeth are lost; **6,** branchiostegal membranes from the left and right sides are fused; **7,** the postcleithrum is lost; **8,** ribs are lost; **9,** rayed pectoral fins absent; **10,** deflection of the anus onto the eyed side.

specialization, trends, "adaptive" radiation, and patterns of functional evolution should be founded on a corroborated set of statements about phylogenetic patterns of structural features. The emphasis on theories of process and evolutionary transformation, for example, has obfuscated the analysis of tetrapod origins throughout this century (Patterson, 1980; Rosen *et al.*, 1981).

If progress in this decade continues at the rapid pace with which problems in ray-finned fish evolution have been solved in recent years, actinopterygians will soon be a model group for the analysis of evolutionary patterns and processes.

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The Postcranial Skeleton of North American Multituberculates

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THE POSTCRANIAL SKELETON OF NORTH AMERICAN MULTITUBERCULATES

DAVID W. KRAUSE[1] and FARISH A. JENKINS, JR.[2]

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ABSTRACT. Multituberculates are an extinct order of nontherian mammals commonly represented by teeth in late Mesozoic and early Tertiary terrestrial deposits. They are generally regarded as the first major mammalian group to have been predominantly herbivorous. The dentition of multituberculates is well known, but studies of their skeletons have been limited by the rarity of associated remains. In this study we describe a postcranial skeleton of *Ptilodus kummae*, the most complete known for a North American multituberculate. In addition, we review other North American multituberculate postcranial materials in an effort to identify the major structural and functional characteristics of the group.

Despite their diversity in size and in dental specializations, multituberculates as far as known exhibit little variability in their postcranial skeleton. This conclusion is based on a comparison of the specimens of *Ptilodus* with material representing or referable to the following genera: *Catopsalis*, *Cimexomys*, *Cimolodon*, *Ectypodus*, *Eucosmodon*, *Meniscoessus*, *Mesodma*, *Stygimys*, and *Taeniolabis*.

Multituberculates possess a number of unusual and even unique postcranial features. These include a scapulocoracoid with a reduced coracoid but without a supraspinous fossa, an enlarged prepollex, a dorsally emarginate acetabulum, a postobturator foramen within the ischiopubic symphysis, a large parafibula, a slender, ventrally directed lateral flange on the proximal end of the fibula, a deep excavation posteriorly beneath the proximal articular surface of the tibia, a specialized tarsal structure (particularly that of the astragalus and calcaneum), and thoracic centra with the anterior epiphysial surface recessed ventrally and bulbous dorsally.

Ptilodus and *Eucosmodon*, the only two genera for which articulated foot bones are known, possess distinctive tarsal adaptations for a range of pedal mobility (especially abduction) characteristic of arboreal mammals that descend trees headfirst. The

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hallux is divergent, and the entocuneiform-metatarsal I joint permitted considerable hallucal abduction and adduction for prehension in a plane independent of the remaining digits. The long, robust tail of *Ptilodus* possessed musculoskeletal features that, in modern mammals, are present in prehensile-tailed forms. We conclude that at least some multituberculates were arboreal.

INTRODUCTION

Multituberculates are an extinct group of nontherian mammals that have been recovered from North America, Europe, and Asia, and whose known range in geologic history extends from the Late Jurassic to the Oligocene (or possibly from the Late Triassic, if the Haramiyidae are multituberculates [Hahn, 1973]). Although multituberculate teeth are common in Late Cretaceous and Paleocene local faunas of North America, jaws and especially skulls are rare. Postcranial bones are also relatively rare, and the postcranial structure of multituberculates is therefore not well understood.

Several partial skeletons and isolated postcranial bones of multituberculates have been described within the past century. In 1973 a well-preserved and nearly complete skeleton of *Ptilodus kummae* was discovered in the Paleocene Ravenscrag Formation of Saskatchewan, a discovery that provided the impetus for this study of the postcranial skeleton of North American multituberculates. Our description centers largely on the specimen of *P. kummae* because of its unusual completeness. We have also reviewed previously published specimens, as well as additional multituberculate elements (some of which are of uncertain generic or specific identity) in order to provide a comprehensive account and a basis for assessing postural, locomotor, and other adaptations.

PREVIOUS WORK ON MULTITUBERCULATE POSTCRANIAL SKELETONS

Multituberculate postcranial bones are at present known only from North America and Asia. A synopsis of published work is given below.

North America

In 1909 Gidley reported the discovery of an incomplete skeleton associated with the skull and lower jaws of *Ptilodus montanus* from the middle Paleocene of Montana. Preserved were a nearly complete cervical vertebra and some fragmentary caudal vertebrae, and parts of a humerus, radius, ulna, femur, tibia, fibula, pelvis, metapodials, and an ungual phalanx. On the basis of this material, Simpson (1926) attempted a reconstruction of multituberculate locomotor and feeding habits, and Jerison (1973) provided estimates of the body length and weight of *Ptilodus* (which have been criticized by Radinsky [1975]).

A well-preserved specimen of the hind limbs and pelvis of an undetermined species of *Eucosmodon* was recovered from early Paleocene deposits in New Mexico and was referred to in several reports (Granger, *in* Broom, 1914; Granger, 1915; Simpson, 1928a). Simpson and Elftman (1928) reconstructed the hind limb and pelvic musculature and made inferences concerning the habits of *Eucosmodon*. Granger and Simpson (1929) added a detailed osteological description of the specimen. Simpson (1937a) briefly compared the postcranial osteology of *Ptilodus* and *Eucosmodon*.

The less complete skeletons and isolated bones of North American multituberculates that have been described are:

1) Cope (1882a): an astragalus and caudal vertebrae of *Taeniolabis taoensis*. The astragalus, redescribed and figured by Cope in 1884a, was later shown by Matthew (1937) to probably belong to a condylarth (it is, at least, undoubtedly therian). Cope (1884a: pl. XXIIIc, figs. 3 and 4; 1884b: fig. 4b,c) also described and figured a humerus and ulna of *T. taoensis*. The ulna exhibits an articulation of the condylar type possessed by multituberculates (Jenkins, 1973).

Sloan (1981: 158), however, is of the opinion that the humeral fragments "are from some indeterminate placental mammal."

2) Cope (1882b): the distal extremity of a humerus of *Meniscoessus conquistus* (figured by Cope, 1884b: fig. 7g; 1888: fig. 9g).
3) Marsh (1889): a scapulocoracoid, the type of *Camptomus amplus*, together with an interclavicle, astragalus, and calcaneum provisionally referred to the same taxon. Serious doubts have been raised about the association and identification of these specimens (Simpson, 1928a,b; McKenna, 1961). Although McKenna (1961) accepted the astragalus and calcaneum as being those of a multituberculate, he regarded the interclavicle as problematical and provisionally referred the scapulocoracoid, the type specimen, to the Marsupialia.

   Marsh (1889) also figured the distal end of a humerus of "*Dipriodon lunatus*," a left semilunar, probably of "*Dipriodon*" *robustus*, and the proximal end of a femur of "*Halodon sculptus*." All three species are now referred to *Meniscoessus robustus* (see Clemens, 1963). The humerus and femur are undoubtedly from a multituberculate; the semilunar does not resemble the bone tentatively identified as a semilunar of *Ptilodus kummae*.
4) Granger and Simpson (1929): several skeletal fragments of *Stygimys teilhardi* including fragments of both ulnae and femora, the right humerus and ilium, the left tibia, a phalanx, and thoracic, sacral, and caudal vertebrae.
5) Simpson (1937b: 737): "Skull . . . with associated femur, ulna, and some other fragments" of *Ptilodus montanus*. The postcranial remains include left and right femora, a lumbar vertebra, a proximal fragment of a phalanx, and the distal end of a left humerus; no ulna is present. The femora are definitely those of a multituberculate, the phalangeal fragment is much too large to belong to the same individual, and the humeral fragment, as Deischl (1964) previously noted, belongs to a therian.
6) McKenna (1961): two partial scapulocoracoids from the Upper Cretaceous Lance Formation of Wyoming, designated as "Lance Type 1" and "Lance Type 2." Clemens (1963) provisionally allocated the Lance Type 1 and Type 2 scapulocoracoids on the basis of size and frequency to *Mesodma formosa* and *Cimolodon nitidus*, respectively.
7) Deischl (1964): Scapulocoracoids, humeri, ulnae, radii, pelves, femora, tibiae, calcanea, and astragali from the Upper Cretaceous Bug Creek Anthills locality, Hell Creek Formation, Montana; these bones were variously assigned, on the basis of size and frequency data, to *Mesodma thompsoni, Mesodma formosa, Cimexomys minor, Cimolodon nitidus, Stygimys kuszmauli*, and *Catopsalis joyneri*. Sloan and Van Valen (1965) reconstructed the skeleton of *Mesodma thompsoni*.
8) Sahni (1972): calcaneum and fragmentary humerus and femur of ?*Mesodma primaeva* and calcaneum of *Meniscoessus major*.
9) Jenkins (1973): a left ulna (unidentified) and a right humerus referred to ?*Catopsalis*, both from the Bug Creek Anthills locality.
10) Jenkins and Weijs (1979): a composite reconstruction of an unidentified multituberculate scapulocoracoid from the Bug Creek Anthills locality.
11) Krause and Baird (1979): left femoral fragment of an unidentified multituberculate from the Mount Laurel Formation, New Jersey.

Asia

References to published work on Asiatic multituberculate postcranial material

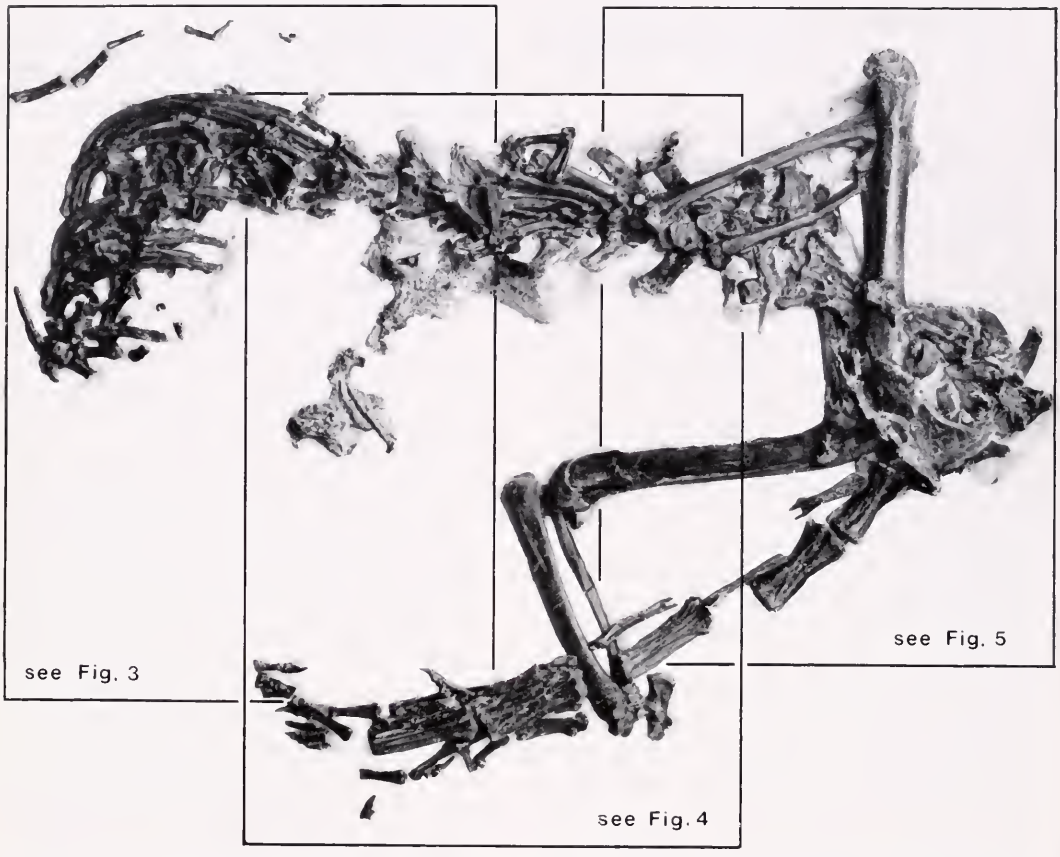

Figure 1. Left side of postcranial skeleton of *Ptilodus kummae* (UA 9001). A key to stereophotographs of specific regions is shown. × 1.28.

are included in this study because these materials offer additional and important insights.

Simpson (1928c: 9) described "several associated foot bones, five fragmentary vertebrae, the lower end of a scapula, a large part of a humerus, ribs and several other fragments" associated with the type skull of *Djadochtatherium matthewi* (AMNH 20440) from the Upper Cretaceous Djadokhta Formation of Mongolia. *Djadochtatherium* Simpson, 1925 is now considered to be a junior synonym of *Catopsalis* Cope, 1882c (Kielan-Jaworowska and Sloan, 1979). McKenna (1961) redescribed the fragmentary scapulocoracoid in his review of the multituberculate shoulder girdle.

Recent discoveries by the Polish-Mongolian Palaeontological Expeditions to Mongolia include postcranial materials of at least four species of multituberculates from the Upper Cretaceous Djadokhta and Barun Goyot formations: a nearly complete skeleton of *Chulsanbaatar vulgaris* and partial skeletons of *Kryptobaatar dashzevegi, Nemegtbaatar gobiensis*, and *Sloanbaatar mirabilis* (Kielan-Jaworowska, 1970, 1974; Clemens and Kielan-Jaworowska, 1979). With the exception of accounts of the pelvis in *K. dashzevegi* (Kielan-Jaworowska, 1969, 1979) and the

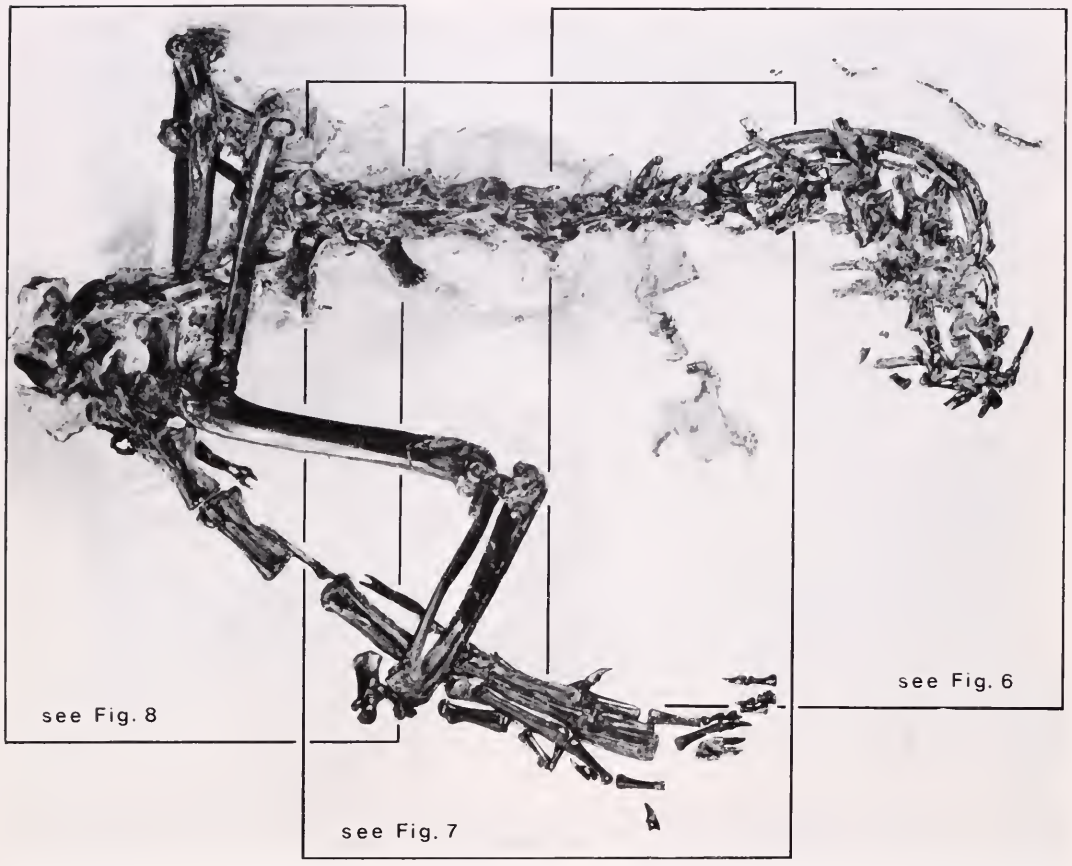

Figure 2. Right side of postcranial skeleton of *Ptilodus kummae* (UA 9001). A key to stereophotographs of specific regions is shown. × 1.28.

partial humeri and left ulna of *Tugrigbaatar saichanensis* from the Toogreeg beds (Kielan-Jaworowska and Dashzeveg, 1978), the material is as yet unpublished. However, Clemens and Kielan-Jaworowska (1979) provided some information on the Mongolian forms (studied by Kielan-Jaworowska) in their brief review of the multituberculate postcranial skeleton. The specimen of *T. saichanensis* is housed in the Institute of Geology of the Mongolian Academy of Sciences in Ulan Bator; all of the rest of this important Asiatic material is in the Institute of Paleobiology (Zakład Paleobiologii) of the Polish Academy of Sciences in Warsaw.

ABBREVIATIONS

Abbreviations used for the names of museums:

AMNH—American Museum of Natural History, New York
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
PU—Princeton University Museum, Princeton, New Jersey
UA—University of Alberta, Edmonton, Alberta
UCMP—Museum of Paleontology, University of California, Berkeley, California

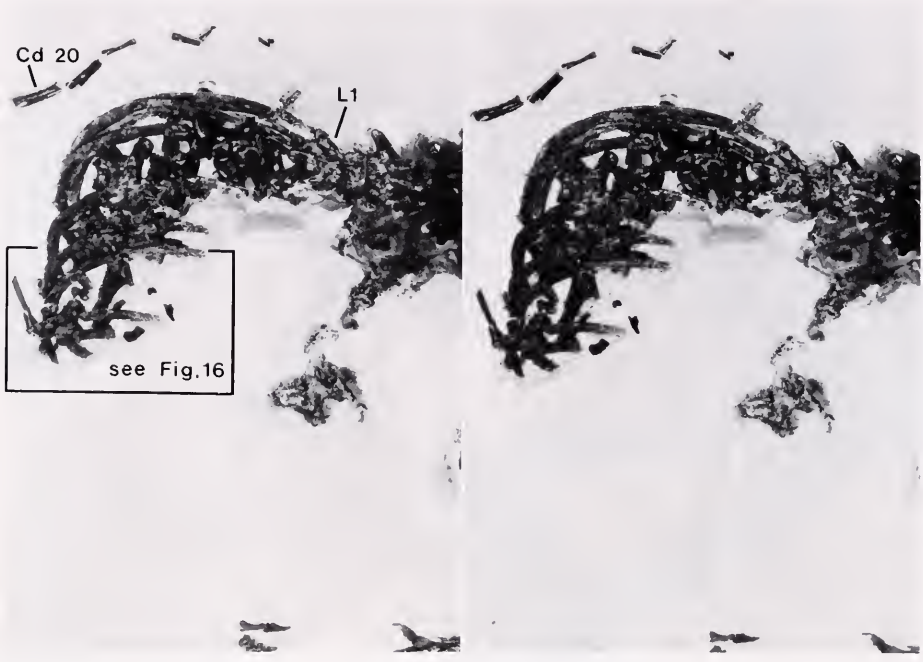

Figure 3. Stereophotographs of anterior portion of left side of postcranial skeleton of *Ptilodus kummae* (UA 9001). The area referenced to Figure 16 contains the ?right carpus. × 1.25.

Abbreviations: *Cd20*, ?twentieth caudal vertebra; *L1*, presumed first lumbar vertebra.

UM—University of Michigan Museum of Paleontology, Ann Arbor, Michigan
UMVP—University of Minnesota, Minneapolis, Minnesota
USNM—United States National Museum, Washington, D.C.
YPM—Peabody Museum of Natural History, Yale University, New Haven, Connecticut

MATERIALS

Type Specimen of *Ptilodus kummae* (UA 9001)

This specimen was discovered at a late Paleocene (Tiffanian) locality (UAR2g; see Krause, 1977) in the Ravenscrag Formation of Saskatchewan. Prior to discovery, the skull, both lower jaws, several anterior vertebrae, the pectoral girdle, most of the forelimbs, and some caudal vertebrae had eroded from the rock. Fragments of these elements were recovered by surface collecting and by washing and screening the surrounding matrix. The fragments thus obtained include several teeth (left I_1 and P^4; right P_4, M_1, and P^{2-4}), the distal end of the right scapulocoracoid, fragments of the right humerus, proximal parts of both radii, a proximal segment of the right ulna, ten manual phalanges, and three caudal vertebrae. Association of these isolated elements with the articulated specimen is confidently established by the close proximity in which they were found, the virtual absence of bone in the immediately adjacent area, the anatomical correspondence to known allotherian skeletal elements (especially those of *Ptilodus montanus* described by Gidley [1909]), the absence of duplication of individual bones, and the close fit of some complex articular surfaces (for example, the humerus and ulna).

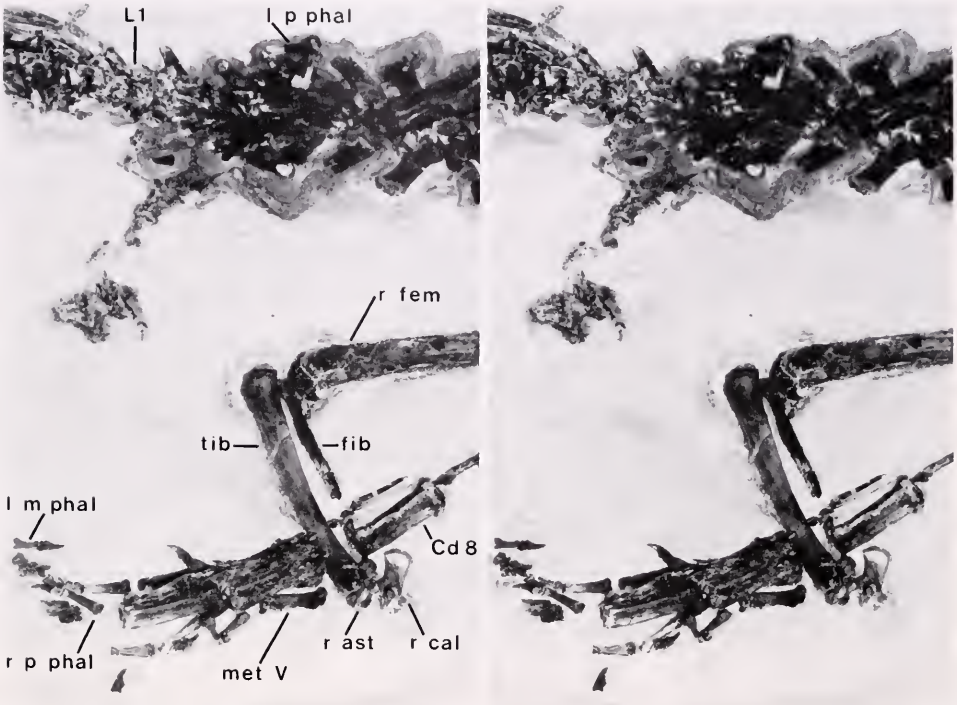

Figure 4. Stereophotographs of central portion of left side of postcranial skeleton of *Ptilodus kummae* (UA 9001). For details of the right tarsal bones, see Figure 27B. × 1.25.

Abbreviations: l, left; *r*, right; *ast*, astragalus; *cal*, calcaneum; *Cd8*, eighth caudal vertebra; *fem*, femur; *fib*, fibula; *L1*, presumed first lumbar vertebra; *m phal*, manual phalanges; *met V*, fifth metatarsal; *p phal*, pedal phalanges; *tib*, tibia.

The specimen as preserved *in situ* lay on its right side. This side was prepared first, and then covered with a white mold-making rubber (Silastic A RTV, Dow Corning Corp.). The specimen was then inverted and the left side prepared, a mold made, and finally embedded in clear Bioplastic (Ward's Natural Science Establishment, Inc.). This technique firmly secured the fragile, delicate bones and permits observation of both sides of the specimen. During preparation, the following bones were removed because they prevented exposure of critical areas of the skeleton: left calcaneum, left ectocuneiform, left metatarsal V, three phalanges of the left pes, a parafibula, and several smaller fragments, primarily pedal sesamoids.

The articulated portion of the skeleton is virtually complete posterior to the anterior part of the rib cage (Figs. 1–8). The only portions of the pectoral limbs remaining intact are a poorly preserved distal segment of the ?right ?radius, most of the ?right carpus (with attached metacarpal and complete digit I, and the proximal portion of metacarpal II), and some middle and distal phalanges of the ?left manus. The long tail had curled around the anterior part of the body. A middle segment of the tail, containing approximately eight vertebrae, had weathered out prior to discovery.

OTHER MATERIAL

All known articulated postcranial remains as well as various disarticulated and

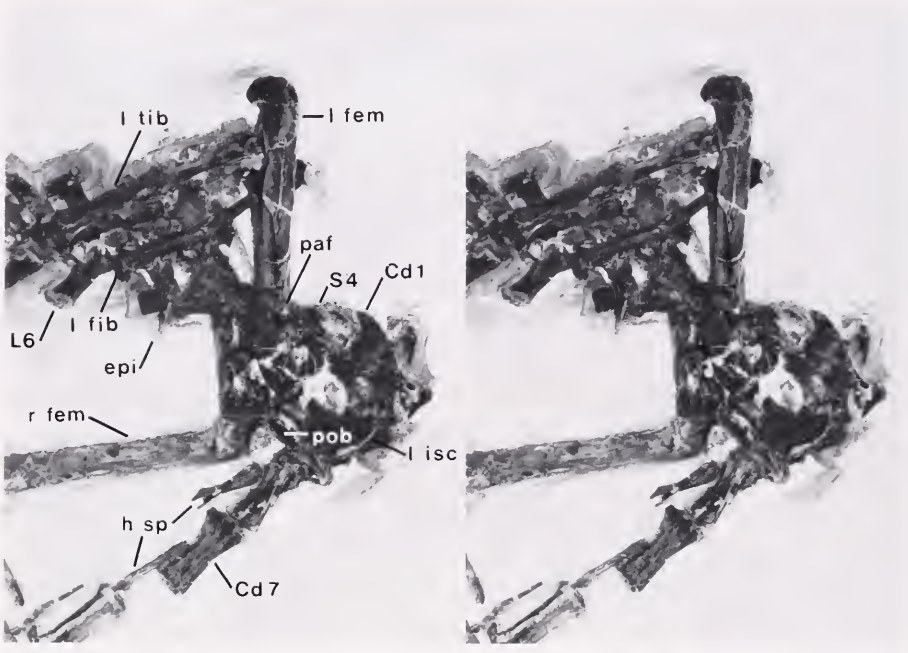

Figure 5. Stereophotographs of posterior portion of left side of postcranial skeleton of *Ptilodus kummae* (UA 9001). ×1.25.
Abbreviations: l, left; *r,* right; *Cd1, Cd7,* first and seventh caudal vertebrae; *epi,* epipubic bone; *fem,* femur; *fib,* fibula; *h sp,* haemal spine; *isc,* ischium; *L6,* sixth lumbar vertebra; *paf,* parafibula; *pob,* postobturator foramen; *S4,* fourth sacral vertebra; *tib,* tibia.

fragmentary bones of North American multituberculates were studied. These were used primarily to describe features that are poorly preserved or missing in the specimen of *P. kummae* (UA 9001). This procedure, however, does not imply that the postcranial elements of different multituberculate taxa were identical in every detail; rather, it provides an outline of basic features, at least for ptilodontoids and taeniolabidoids. On present evidence, structural variability among ptilodontoid and taeniolabidoid postcranial bones is not so great as to diminish the utility of describing and making functional interpretations of a basic plan.

Definite generic and specific assignments of postcranial elements are possible only on the basis of associated dental material. Accordingly, we preface with a question mark all taxonomic allocations of isolated elements or partial skeletons that lack dental remains. Materials of the following taxa, grouped according to locality, were available for this study:

1) Irvine locality, Late Cretaceous (Judithian), Judith River Formation, Alberta. Isolated elements (UA collections) not assigned to specific taxa.
2) Clambank Hollow locality, Late Cretaceous (Judithian), Judith River Formation, Montana. Isolated elements (AMNH collections) assigned by Sahni (1972) to ?*Mesodma primaeva* and *Meniscoessus major.*
3) Upper Hop Brook locality, Late Cretaceous, Mount Laurel Formation, New Jersey. Isolated femoral fragment (PU 21451) of an unidentified multituberculate (Krause and Baird, 1979).
4) Lull 2 Quarry (UCMP locality V-5620) and localities of uncertain location (Marsh, 1889; McKenna, 1961),

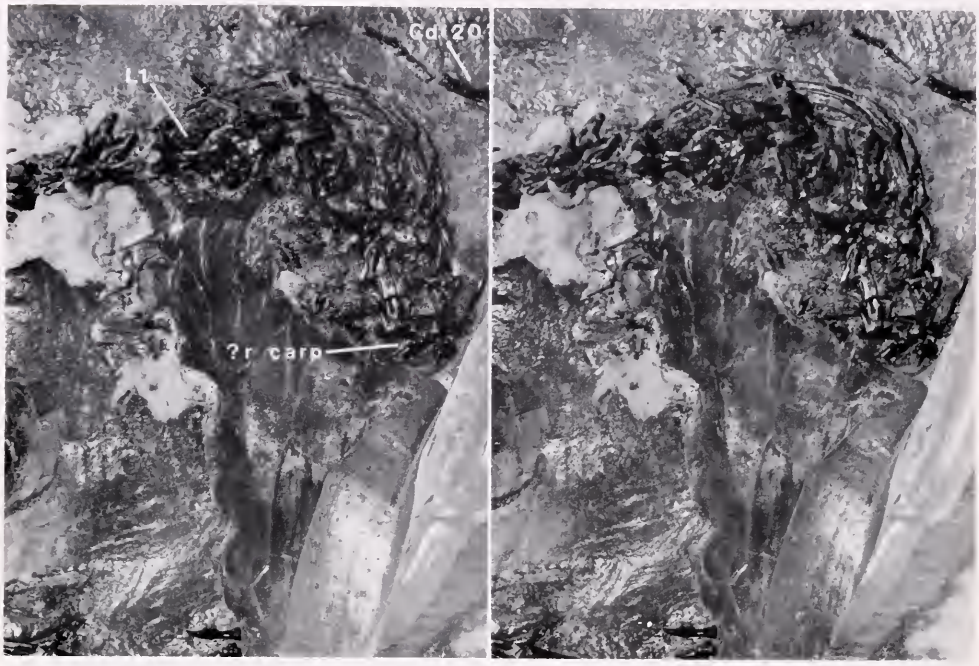

Figure 6. Stereophotographs of anterior portion of right side of postcranial skeleton of *Ptilodus kummae* (UA 9001). × 1.25. *Abbreviations: ?r carp*, ?right carpus; *Cd20*, ?twentieth caudal vertebra; *L1*, presumed first lumbar vertebra.

Late Cretaceous (Lancian), Lance Formation, Wyoming. Isolated elements in AMNH and YPM collections tentatively allocated to *Mesodma formosa*, *Cimolodon nitidus*, and *Meniscoessus robustus* (Clemens, 1963).

5) Type locality of *Meniscoessus conquistus*, Late Cretaceous (Lancian), "Laramie Formation," South Dakota. Humeral fragment (AMNH 3011a) of *Meniscoessus conquistus* (Cope, 1882b).
6) Bug Creek Anthills locality, Late Cretaceous (Lancian), Hell Creek Formation, Montana. Many isolated elements in AMNH, MCZ, UA, UCMP, and UMVP collections. The UMVP collections include bones referred to *Mesodma thompsoni*, *Mesodma formosa*, *Cimexomys minor*, *Cimolodon nitidus*, *Stygimys kuszmauli*, and *Catopsalis joyneri* by Deischl (1964). In a study of intrageneric variation of *Mesodma*, Novacek and Clemens (1977) found that *M. thompsoni* and *M. formosa* at the Bug Creek Anthills locality could not be distinguished on the basis of dentitions; our referrals of postcranial elements to this taxon are therefore designated as ?*Mesodma* sp.
7) Mantua Quarry, early Paleocene (Puercan), Fort Union Formation, Wyoming. Isolated calcaneum (PU 14487) of an unidentified multituberculate.
8) Uncertain locality in San Juan Basin, early Paleocene (Puercan), Nacimiento Formation, New Mexico. Ulnar fragment (AMNH 3036) of ?*Taeniolabis taoensis* (Cope, 1882a).
9) Locality 3 miles east of Kimbetoh, San Juan Basin, early Paleocene (Puercan), Nacimiento Formation, New Mexico. Nearly complete hind limbs and pelvis (AMNH 16325) of ?*Eucosmodon* sp. (Granger, 1915; Simpson

Figure 7. Stereophotographs of central portion of right side of postcranial skeleton of *Ptilodus kummae* (UA 9001). For details of the right tarsal bones, see Figure 27A. × 1.25.

Abbreviations: cal, calcaneum; *Cd8,* eighth caudal vertebra; *fem,* femur; *fib,* fibula; *h sp,* haemal spine; *L2, L5,* second and fifth lumbar vertebrae; *m phal,* manual phalanges; *met V,* fifth metatarsal; *pat,* patella; *tib,* tibia.

and Elftman, 1928; Granger and Simpson, 1929; Simpson, 1937a).

10) Torrejon Arroyo, San Juan Basin, middle Paleocene (Torrejonian), Nacimiento Formation, New Mexico. Associated dentaries and skeletal fragments (AMNH 16024) of *Stygimys teilhardi* (Granger and Simpson, 1929).
11) Gidley Quarry, middle Paleocene (Torrejonian), Fort Union Formation, Montana. Skull and several associated skeletal fragments (AMNH 35490) of *Ptilodus montanus* (Simpson, 1937b) and a left proximal humerus (USNM 9735) of ?*Ptilodus montanus.*
12) Silberling Quarry, middle Paleocene (Torrejonian), Fort Union Formation, Montana. Skull, dentaries and incomplete skeleton (USNM 6076) of *Ptilodus montanus* (Gidley, 1909; Simpson, 1937a,b).
13) Locality UAR2g, late Paleocene (Tiffanian), Ravenscrag Formation, Saskatchewan. Several isolated fragments (UA collections) of ?*Ptilodus kummae.*
14) UM locality SC-195, early Eocene (Clarkforkian), Willwood Formation, Wyoming. Associated dentition and skeletal fragments (UM 69868) of *Ectypodus powelli.*
15) UM locality SC-188, early Eocene (Clarkforkian), Willwood Formation, Wyoming. Isolated elements (UM collections) of unidentified multituberculate(s).
16) UM locality SC-210, early Eocene

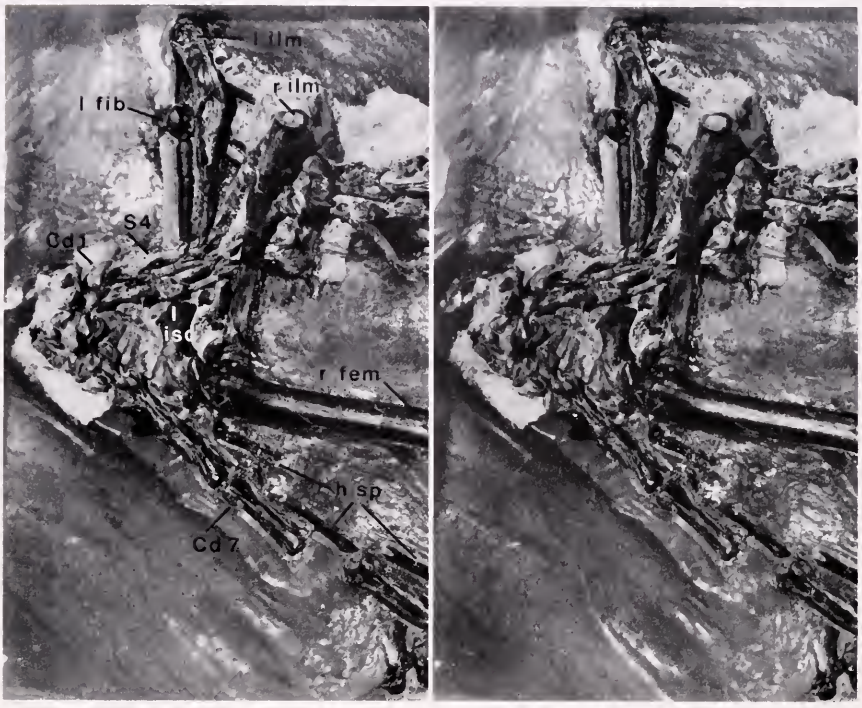

Figure 8. Stereophotographs of posterior portion of right side of postcranial skeleton of *Ptilodus kummae* (UA 9001). × 1.25. *Abbreviations: l*, left; *r*, right; *Cd1, Cd7*, first and seventh caudal vertebrae; *fem*, femur; *fib*, fibula; *h sp*, haemal spines; *ilm*, ilium; *isc*, ischium; *S4*, fourth sacral vertebra.

(Wasatchian), Willwood Formation, Wyoming. Humeral fragment (UM 74674) of ?*Ectypodus tardus*.

OSTEOLOGY OF THE APPENDICULAR SKELETON

SCAPULOCORACOID

(Figures 9, 10)

UA 9001—A fragment of the right scapulocoracoid preserves most of the glenoid but little of the blade; the coracoid is broken off (Fig. 9B). The glenoid is a shallow, pyriform fossa, broadest posteriorly and tapering toward the coracoid suture.

On the costal surface of the scapula is a low crest that arises near the medial rim of the glenoid fossa and extends posterodorsally for approximately 3 mm. A shallow fossa and nutrient foramen occur on the posteromedial aspect of the blade adjacent to the glenoid.

Other material—?*Mesodma* sp. (UA 11992), distal fragment; ?*Mesodma* sp. (UA 11993), distal fragment lacking coracoid process; Multituberculata indet. (MCZ 20785), distal fragment lacking coracoid process and scapular spine; Multituberculata indet. (UMVP 1400), distal fragment lacking coracoid process and scapular spine.

UA 11992 has a complete coracoid (Fig. 10C,D) that is synostosed to the scapula; no suture can be seen. Distally, the coracoid is transversely expanded to a slight degree. The scapular and coracoid parts of the glenoid thus form an arcuate (approximately 90°) surface to receive the humeral head.

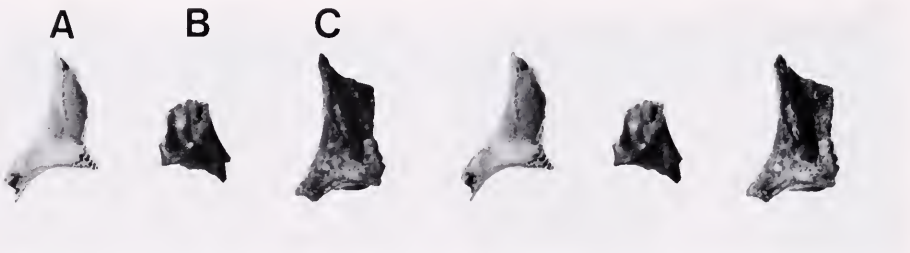

Figure 9. Stereophotographs of scapulocoracoids of North American Multituberculata. A) MCZ 20785, Multituberculata indet., Bug Creek Anthills locality, left distal fragment missing coracoid process, lateral view; B) UA 9001, *Ptilodus kummae,* locality UAR2g, right distal fragment missing coracoid process, lateral view; C) UMVP 1400, Multituberculata indet., Bug Creek Anthills locality, left distal fragment missing coracoid process, lateral view. × 2.2.

The narrow scapular blade is partially preserved in several specimens from the Late Cretaceous (Figs. 9A,C, 10). The infraspinous fossa occupies the lateral surface as a deep sulcus. The anterior margin of the sulcus is a laterally projecting flange, the homologue of the scapular spine. In one specimen (UA 11992) the ventral (acromial) part of the spine is reflected posteriorly, probably relating to the attachment of the deltoid. The acromion is not preserved in any available specimen.

Clavicle and Interclavicle

No clavicle or interclavicle of a multituberculate has been positively identified. The fragmentary interclavicle (YPM

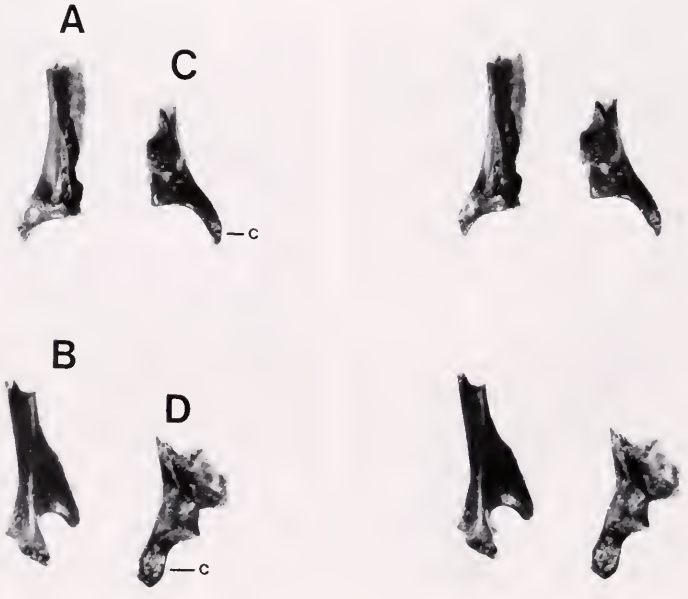

Figure 10. Stereophotographs of scapulocoracoids of ?*Mesodma* sp., Bug Creek Anthills locality. A) and B) UA 11993, left distal fragment missing coracoid process in lateral and anterior view; C) and D) UA 11992, right distal fragment in lateral and posterior views (in this specimen the coracoid process (*c*) is complete). × 4.0.

10639) described by Marsh (1889) is enigmatic. The specimen's supposed association with a calcaneum, astragalus, and partial scapulocoracoid has been questioned (Simpson, 1928a,b; McKenna, 1961). McKenna (1961) provisionally referred the scapulocoracoid to the Marsupialia, and we find that the calcaneum and especially the astragalus differ in major features from the pattern known in *Ptilodus* and ?*Eucosmodon* (see below). We do not doubt that the specimen in question is an interclavicle, but without comparative material have no basis for confirming or denying that it represents that of a multituberculate.

Humerus

(Figures 11, 12)

UA 9001—The humeri are represented by fragments from the heads, a partial right diaphysis, and a fragment of the distal end of the right humerus.

The large and spherical radial condyle (capitulum) is ventrally directed. Dorsal to the condyle is a broad linear ridge that runs proximodistally and forms the lateral margin of the intercondylar groove. Ventrally, a shallow groove separates the radial condyle from the ectepicondyle. The ulnar condyle, separated from the radial condyle by the wide intercondylar groove, is elongate and wraps around the distal end of the humerus. The extensor (dorsal) surface is situated more laterally than the flexor surface, and thus has a "spiral" configuration (Jenkins, 1973).

Other Material—?*Catopsalis joyneri* (MCZ 19529), right distal fragment; ?*Cimexomys minor* (UMVP 1404), left distal fragment; ?*Ectypodus tardus* (UM 74674), right distal fragment; ?*Meniscoessus conquistus* (AMNH 3011a), left distal fragment; ?*Meniscoessus robustus* (YPM 10612a), left distal fragment; ?*Mesodma primaeva* (AMNH 77175), right distal fragment; ?*Mesodma* sp. (MCZ 20789), left distal fragment; ?*Mesodma* sp. (MCZ 20786, MCZ 20787, MCZ 20788, UMVP 1405, UMVP 1406), right distal fragments; ?*Mesodma* sp. (UMVP 1403), distal two-thirds of left humerus; ?*Ptilodus kummae* (UA 11300), right distal epiphysis; *Ptilodus montanus* (USNM 6076), nearly complete but damaged left humerus; ?*Ptilodus montanus* (USNM 9735), left proximal humerus; ?*Stygimys kuszmauli* (UA 11994), distal half of right humerus; ?*S. kuszmauli* (UMVP 1407), left distal humerus; ?*Stygimys teilhardi* (AMNH 16024), right radial condyle.

The best preserved proximal humerus of a North American form is problematical in its association; the specimen was found in the same box with a maxilla (USNM 9735) of *Ptilodus montanus* from Gidley Quarry, but no records attest to its actual association. That it is multituberculate is established by its resemblance to the proximal humerus of *Tugrigbaatar saichanensis* figured by Kielan-Jaworowska and Dashzeveg (1978). The specimen possesses robust greater and lesser tuberosities and a bulbous, ovoid head that is reflected proximodorsally (Fig. 11A,B,C).

The linear ulnar condyle, in distal view, intercepts the interepicondylar axis at an angle of approximately 72° on the humeral fragment of ?*Ptilodus kummae* (UA 11300) as well as on that of *P. montanus* (USNM 6076). The entepicondyle is not preserved on either UA 9001, UA 11300, or USNM 6076, but a distinct groove separates it from the ulnar condyle. More nearly complete humeri of multituberculates recovered from the Bug Creek Anthills locality in UMVP and UA collections show that the entepicondyle is much larger than the ectepicondyle; the entepicondyle projects distomedially as a broad, dorsoventrally depressed flange and is pierced by a large entepicondylar foramen (see also Jenkins, 1973, fig. 19).

A complete humerus is not known for any North American multituberculate. The most complete specimen available (*Ptilodus montanus*, USNM 6076; Fig. 11H,I) reveals a well-developed deltopectoral crest and a nearly hemispherical humeral head (breakage precludes determining its exact orientation). The lateral surface of the deltopectoral crest and the dorsal surface of the shaft have an angular intersection, thus forming a distinctive ridge running proximodistally from the

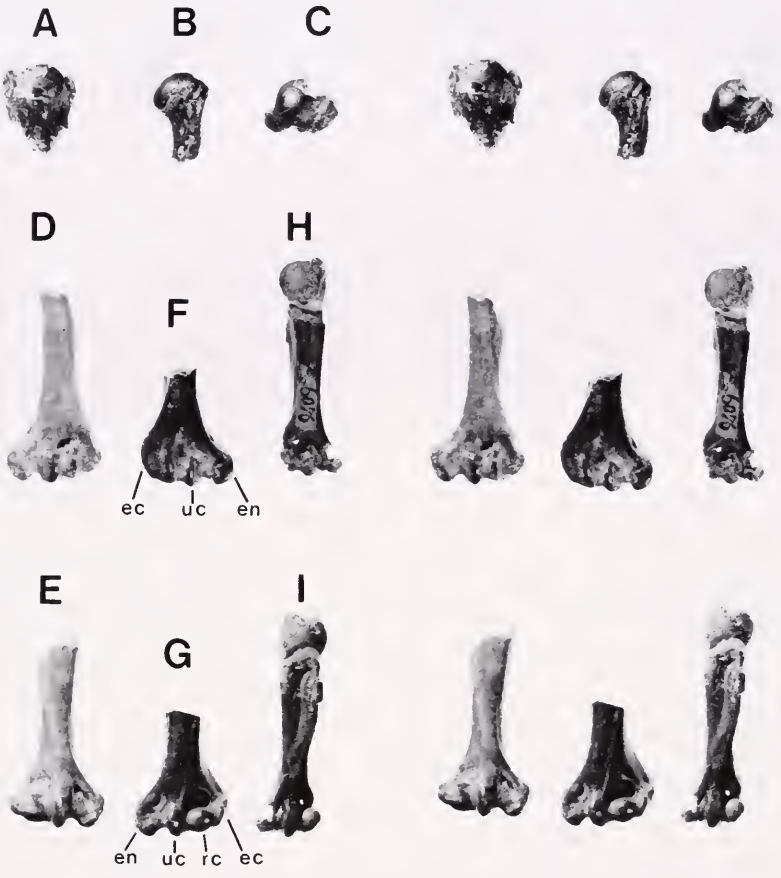

Figure 11. Stereophotographs of humeri of North American Multituberculata. A–C) USNM 9735, ?*Ptilodus montanus*, Gidley Quarry, left proximal humerus in dorsal, medial and proximal views. The articular surface adjacent to the greater tuberosity has been damaged. D) and E) UA 11994, ?*Stygimys kuszmauli*, Bug Creek Anthills locality, right distal fragment in dorsal and ventral views; F) and G) UMVP 1407, ?*Stygimys kuszmauli*, Bug Creek Anthills locality, left distal fragment in dorsal and ventral views; H) and I) USNM 6076, *Ptilodus montanus*, Silberling Quarry, nearly complete but damaged left humerus (head is affixed with clay) in dorsal and ventral views. × 1.5.

Abbreviations: ec, ectepicondyle; *en*, entepicondyle; *rc*, radial condyle; *uc*, ulnar condyle.

humeral head to the ectepicondylar flange (the "posterior crest" of Kielan-Jaworowska and Dashzeveg, 1978). The proportions of the humerus represented in Figure 31 are based in part on USNM 6076 in which the head is separated from the shaft; it is possible that part of the shaft has been lost at the fracture. A reconstruction of the humerus of *Tugrigaatar saichanensis* by Kielan-Jaworowska and Dashzeveg (1978) depicts a more gracile, elongate bone.

Ulna

(Figures 13, 14)

UA 9001—The right ulna is represented by a fragment representing the olec-

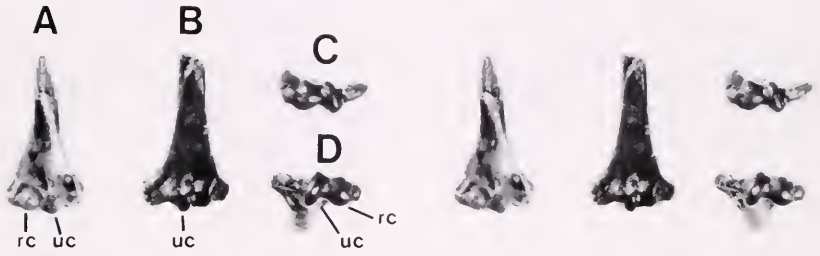

Figure 12. Stereophotographs of humeri of ?*Mesodma* sp., Bug Creek Anthills locality. A) MCZ 20788, right distal fragment, ventral view; B) MCZ 20787, right distal fragment, dorsal view; C) MCZ 20789, left distal fragment, distal view; D) MCZ 20786, right distal fragment, distoventral view. × 3.0.

Abbreviations: rc, radial condyle; *uc*, ulnar condyle.

ranon and proximal part of the semilunar notch (Fig. 13B).

The olecranon is laterally compressed. The medial margin of the apex bears an excrescence, and therefore the olecranon is somewhat asymmetrical. The articular surface for the capitulum is a shallowly concave facet restricted to the dorsolateral corner of the semilunar notch. The articular surface for the ulnar condyle is nearly semicircular; proximally, the facet is deeply recessed, but distally is almost flat from medial to lateral side. The proximodistal axis of this facet is obliquely oriented (estimated at about 10°) to the ulnar shaft. A prominent crest is formed at the intersection of the two facets and is also oriented slightly obliquely to the axis of the ulnar shaft (from proximolateral to distomedial aspect); it articulates with the intercondylar groove on the humerus. A prominent anconeal process is accommodated by a deep olecranon fossa on the humerus.

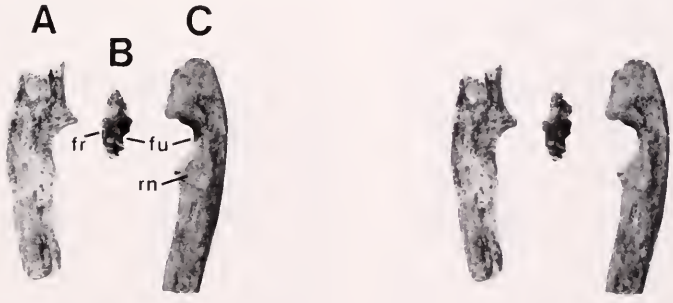

Figure 13. Stereophotographs of ulnae of North American Multituberculata. A) UMVP 1412, ?*Catopsalis joyneri*, Bug Creek Anthills locality, left proximal fragment missing part of olecranon process, anteromedial view; B) UA 9001, *Ptilodus kummae*, locality UAR2g, right proximal fragment, anterior view; C) MCZ 19527, ?*Catopsalis joyneri*, Bug Creek Anthills locality, left proximal fragment missing part of olecranon process, lateral view. × 1.5.

Abbreviations: fr, facet for radial condyle; *fu*, facet for ulnar condyle; *rn*, radial notch.

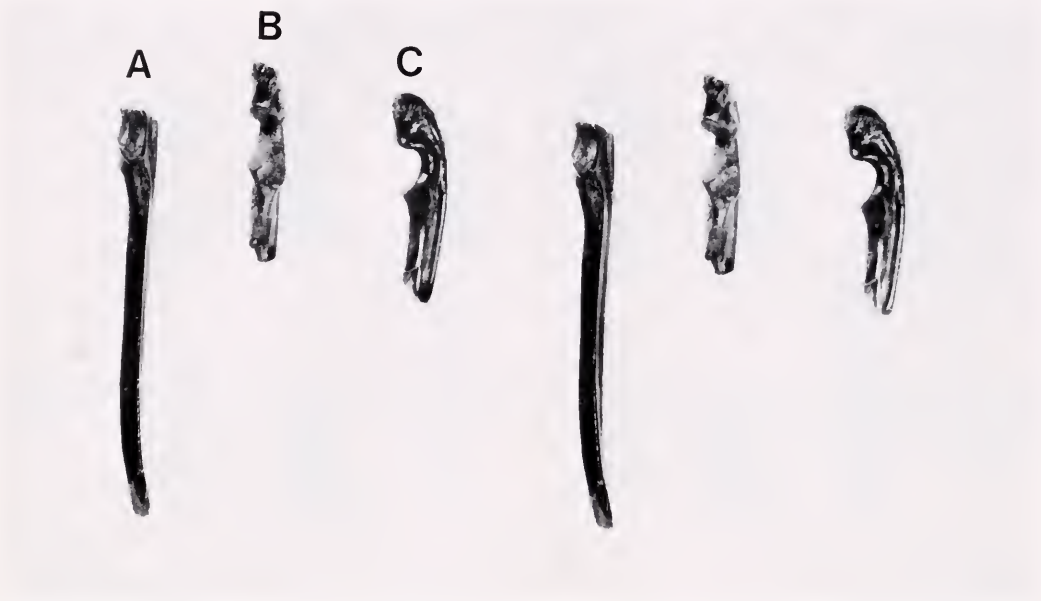

Figure 14. Stereophotographs of ulnae of ?*Mesodma* sp., Bug Creek Anthills locality. A) UMVP 1414, right ulna missing proximal and distal ends, anterior view; B) MCZ 20780, left proximal fragment, anterior view; C) MCZ 20781, left proximal fragment, lateral view. × 4.2.

Other Material—?*Ptilodus kummae* (UA 11302), distal half of semilunar notch and proximal part of shaft; *Stygimys teilhardi* (AMNH 16024), two olecranons including proximal half of semilunar notch; ?*S. kuszmauli* (UMVP 1411), proximal right ulna; ?*Mesodma* sp. (UMVP 1413), left semilunar notch and olecranon; ?*Mesodma* sp. (UMVP 1409), proximal right ulna; ?*Mesodma* sp. (UMVP 1410), proximal right ulna; ?*Mesodma* sp. (UMVP 1414), distal half of semilunar notch and all of shaft except distal end; ?*Mesodma* sp. (MCZ 20780, MCZ 20781), left proximal fragments; ?*Catopsalis joyneri* (UMVP 1412), proximal half of left ulna; ?*Catopsalis joyneri* (MCZ 19527), proximal left ulna missing part of olecranon; ?*Cimexomys minor* (UMVP 1408), semilunar notch of left ulna; ?*Taeniolabis taoensis* (AMNH 3036), semilunar notch of right ulna.

The radial notch is an oval, shallowly concave facet distal to the articular surface for the radial condyle.

Distal to the semilunar notch the ulnar shaft narrows transversely. A longitudinal fossa, bordered medially by a ridge, occurs on the flexor surface of the shaft just distal to the coronoid process.

An ulnar shaft (UMVP 1414) referable to ?*Mesodma* sp. has a cross section in the form of an isosceles triangle, with the base representing the anterior surface and the apex the posterior margin (Fig. 14A). Distally the shaft curves medially, tapers, and becomes more or less cylindrical. A distal articular surface has not yet been positively identified.

Radius
(Figure 15)

UA 9001—The radii of *P. kummae* are represented by the head from the left side, and the proximal half from the right. Associated with the ?right carpus is a crushed distal radius that preserves no diagnostic features.

The head of the radius is elliptical in outline. The concave capitular facet is also elliptical, that is, longer anteroposteriorly than transversely. However, the concavity of the articular surface is spheroidal. A strap-shaped facet that articulates with the

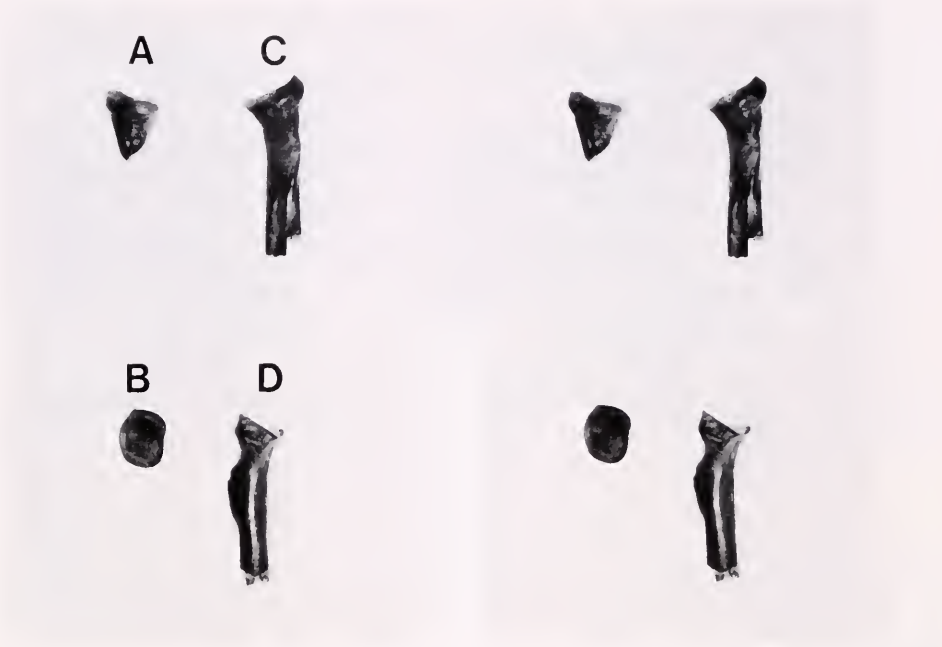

Figure 15. Stereophotographs of radii of *Ptilodus kummae* (UA 9001), locality UAR2g. A) and B) left proximal fragment in medial and proximal (top is posterior) views; C) and D) right proximal fragment in medial and lateral views. × 2.7.

ulna extends for approximately 90° around the posteromedial margin of the radial head. The anterolateral margin of the radial head bears an elongate, flat facet that opposes a shallow groove between the ectepicondyle and the radial condyle of the humerus.

The proximal part of the shaft is mediolaterally compressed. Distal to the ulnar facet is a longitudinal ridge, the anterior surface of which is rugose and probably marks the insertion of the biceps brachii. The angular anteromedial margin of the shaft may represent the attachment of a radioulnar interosseous membrane.

Other Material—?*Mesodma* sp. (UMVP 1416), proximal half of right radius; ?*Catopsalis joyneri* (UMVP 1438, UMVP 1439), proximal halves of left radii; *Ptilodus montanus* (USNM 6076), right radius lacking distal end.

These specimens share the same basic features with the proximal radii of *Ptilodus kummae*.

MANUS
(Figures 3, 6, 16)

UA 9001—A partial and slightly disarticulated manus is preserved (Fig. 16). The interpretation that it is a right manus, and the identification of the individual ossicles, are not absolutely certain. The single complete metacarpal (5.3 mm in length) we regard as pollical, and on this assumption have been able to suggest the identity of the other elements. This interpretation is based on three observations: the pollical metacarpal appears to be associated with two phalanges only; the pollical metacarpal is in articulation with another metacarpal (II?) at a greater angle of divergence (ca. 40°) than would be expected if it were metacarpal V of the left side; and the adjacent ossicle (prepollex), although elongate, is too small and of an unlikely structure for a pollical metacarpal (see below).

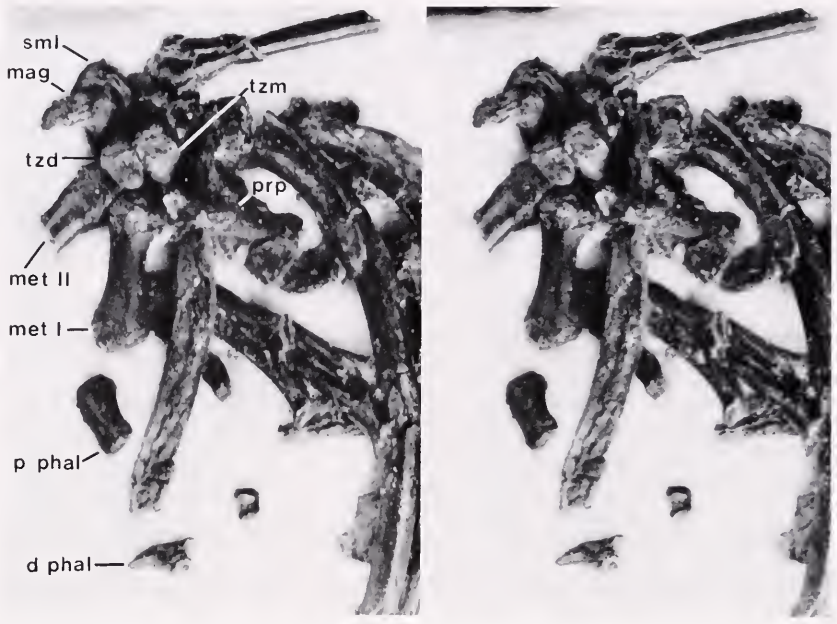

Figure 16. Stereophotographs of dorsal view of partial ?right manus of *Ptilodus kummae* (UA 9001). × 4.4.

Abbreviations: d phal, distal phalanx; *mag,* magnum; *met I, II,* first and second metacarpals; *prp,* prepollex; *p phal,* proximal phalanx; *sml,* semilunar; *tzd,* trapezoid; *tzm,* trapezium.

As preserved, the carpus consists of a damaged distal radius, semilunar (lunate), magnum (capitate), trapezoid, trapezium, and prepollex. The semilunar is a crescentic ossicle, with a concave distal articular surface lying in close contact with the bulbous head of the magnum. The trapezoid is displaced from the magnum, but when articulated their proximal surfaces would be contiguous. Distally, the trapezoid articulates with metacarpal I and a lateral portion of the proximal articular surface of metacarpal II. The trapezium, roughly equivalent to the trapezoid in size, has been displaced from its normal position. The elongate prepollex (2.8 mm in length) is expanded at both ends and appears to have articulated with both the trapezium and pollical metacarpal. The long axes of the proximal and distal ends are at nearly right angles. The distal end, although rounded, does not have the condylar shape typical of a metacarpophalangeal articulation.

The proximal end of metacarpal II is transversely narrower, and its shaft more slender, than that of the pollical metacarpal.

The distal (ungual) and proximal phalanges of the right pollex appear to be associated (Fig. 16). The proximal phalanx is 2.6 mm long and, at midshaft, is 1.1 mm in width. Both the proximal base and, to a lesser extent, the distal end are expanded relative to the transverse diameter of the shaft. The base is dorsoventrally expanded. The head, in dorsal profile, is very slightly convex, bearing no median groove.

The distal phalanx, 2.4 mm long, has a proximal facet that is deeply concave in side view. Both the extensor process and the flexor tubercle are well developed. The flexor tubercle is low, rounded, and is separated from the articular surface by a fossa into which opens a large, distally directed nutrient foramen. The ungual process for support of the claw is slightly recurved and bears a longitudinal, often

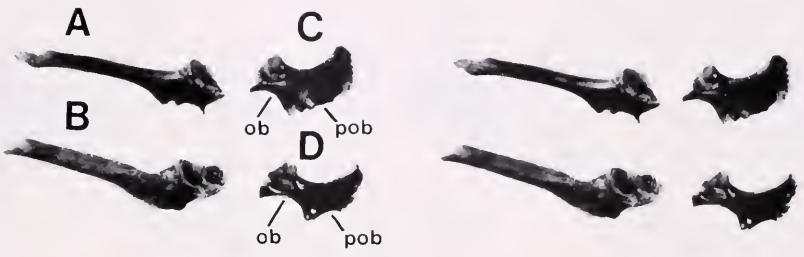

Figure 17. Stereophotographs of pelvic bones of ?*Mesodma* sp., Bug Creek Anthills locality. A) UMVP 1418, partial left ilium, lateral view; B) UMVP 1420, partial left ilium and acetabular facet of the ischium, lateral view (in both specimens part of the pubis is represented along the inferior margin of the acetabulum); C) UMVP 1419, left ischial fragment, lateral view; D) UMVP 1417, left ischial fragment, lateral view. × 2.2.

Abbreviations: ob, dorsal margin of obturator foramen; *pob*, dorsal margin of postobturator foramen.

rugose groove along its dorsomedial and dorsolateral aspects (the dorsolateral groove is longer and deeper). The ungual process is slightly constricted transversely near midlength, expands distally, and tapers to a pointed terminus.

Three middle and three distal phalanges of the ?left manus are preserved in articulation near the distal end of the right pes (Figs. 4, 7). Their digital identity cannot be determined. They are similar in morphology to the pollical phalanges described above but are of different lengths.

PELVIS

(Figures 5, 8, 17, 18)

UA 9001—Both ilia and the left ischium of UA 9001 are preserved intact; the right ischium and both pubes are crushed (Figs. 5, 8). Pelvic sutures appear to have been firmly synostosed.

The long, rodlike ilium is reflected laterally at its anterior end. The ilium is elliptical in cross-section except at the expanded auricular surface and adjacent to the anterior rim of the acetabulum where it is bladelike. The ventral margin of the ilium adjacent to the acetabulum bears a flange that merges with the pubis below. The lateral surface of the ischium is flat, the medial surface convex. The dorsal margin, rather than straight, recurves sharply to a dorsally directed ischial tuberosity. Although the acetabula are obscured by the articulated femoral heads, the superior margin is recessed and open dorsally by virtue of a lack of contact between the iliac and ischial facets.

Distortion of both pubes and the right ischium, and the fact that the ventral part of the left ischium is almost completely covered by overlying bone, obscures the obturator region. However, it appears that posterior to the obturator foramen lies another, smaller foramen, hereafter referred to as the postobturator foramen.

The obturator foramen is situated directly ventral to the acetabulum, its anterior margin lying at approximately the same level as the anterior margin of the acetabulum. Ventrally, it appears to have been bounded by a thin lamina of bone that is not preserved in any other multituberculate specimen. Deformation precludes precise measurement of the foramen although in anteroposterior length it appears to have been close to 4 mm.

The postobturator foramen is separated from the obturator foramen by a plate of bone approximately 2 mm wide (anteroposteriorly). The foramen itself is approx-

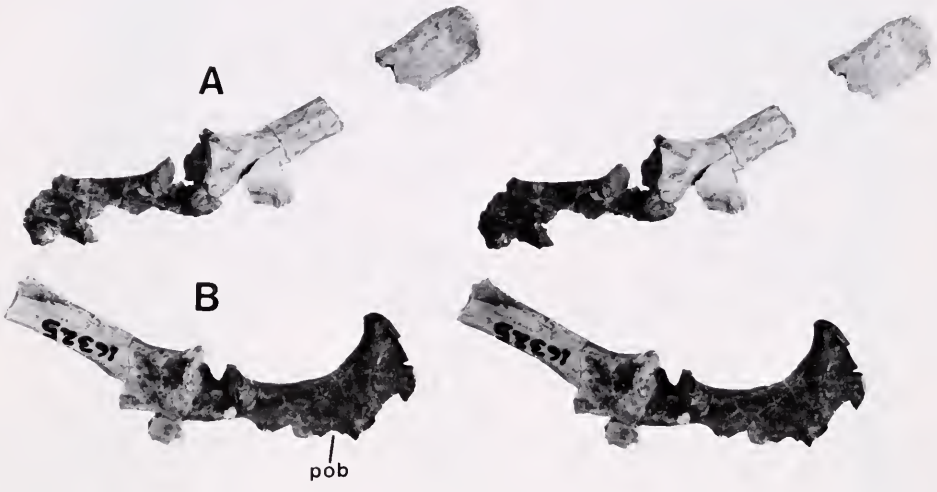

Figure 18. Stereophotographs of pelvis of *?Eucosmodon* sp. (AMNH 16325), San Juan Basin. A) fragmentary right ilium and ischium, lateral view; B) fragmentary left ilium and ischium, lateral view. × 1.25.

Abbreviations: pob, dorsal margin of postobturator foramen.

imately 2.5 mm wide and about 2 mm high; although breakage has occurred, it appears to have been bordered ventrally by a very thin lamina of bone. The postobturator foramen does not open into the pelvic cavity, but rather represents a hiatus in a keel-like ischio-pubic symphysis.

The pubis forms the anterior and part of the ventral border of the obturator foramen. Details of its shape, including the possible presence of facets for epipubic bones, have been lost by postmortem crushing and breakage.

Two elongate, boomerang-shaped bones are located near the right ilium and left ischium, respectively. One end tapers, the other terminates in a slight swelling. A longitudinal sulcus traverses the length of one side of the shaft. These features are similar to those characteristic of the bones that Jenkins and Parrington (1976) identified tentatively as the clavicles of *Eozostrodon*. The possibility that these are clavicles appears to be remote because no other elements of the anterior limb skeleton of *Ptilodus* were so displaced. Rather, it is likely that these are epipubes, and that Jenkins and Parrington's identification may be in error.

Other Material—*?Eucosmodon* sp. (AMNH 16325), nearly complete pelvis including parts of both ilia and ischia, the pubes represented only by bone in region of iliopubic junction; *?Mesodma* sp. (UMVP 1419), partial left ischium; *?Mesodma* sp. (UMVP 1420), nearly complete left ilium lacking anterior tip of blade but including entire acetabulum; *?Mesodma* sp. (UMVP 1417), partial left ischium; *?Mesodma* sp. (UMVP 1418), nearly complete left ilium preserving iliac facet of acetabulum and part of auricular surface; *Ptilodus montanus* (USNM 6076), fragmentary left ilium; *Stygimys teilhardi* (AMNH 16024), right iliac fragment preserving iliac facet.

The acetabular articular surface, unlike that of therian mammals, is highly asymmetrical. The anterior and largest part of the surface is made up of iliac and pubic contributions; the sutural contacts are

Figure 19. Stereophotographs of femora of North American Multituberculata. A) UA 11301, ?*Ptilodus kummae*, locality UAR2g, left proximal fragment, proximal view; B) AMNH 16024, *Stygimys teilhardi*, Torrejon Arroyo, right distal fragment, distal view. × 2.1.

Abbreviations: fov, fovea capitis femoris.

obliterated in UMVP 1420, but a slight indentation of the acetabular margin and different textural features of the articular surface are here interpreted as marking the iliopubic junction (Fig. 17B). The superior margin of the acetabulum between the ilium and ischium is deeply emarginated. An acetabular fossa and notch are well developed. Similar features are present in ?*Eucosmodon* sp. (AMNH 16325) although details are obscured by breakage (Fig. 18).

Further evidence for a postobturator foramen is evident in UMVP 1419 and UMVP 1417 (Figs. 17C,D), where the dorsal margins of both the obturator and postobturator foramina are separated by a cylindrical bony rod of small diameter. The ventral margins of neither foramen are preserved, however. In AMNH 16325 the dorsal margins of both the obturator and the postobturator foramina are also present. In both ?*Eucosmodon* sp. (AMNH 16325) and ?*Mesodma* sp. (UMVP 1419 and 1417) the postobturator foramen is developed within the ischial part of the ischiopubic symphysis and thus is an unpaired, midline feature. Whether or not the foramen had a bony ventral margin as appears to have been the case in *Ptilodus kummae*, or was a hemicircular incisure of the ischial rami, cannot be determined from available materials. Association of the foramen with the origin of an adductor muscle is indicated by the surrounding fossa on the lateral surface (Fig. 17C,D).

The indentation along the ventral margin of the ischium of *Kryptobaatar dashzevegi* posterior to the obturator foramen may represent a postobturator foramen (Kielan-Jaworowska, 1969: fig. 1A; 1979: fig. 1a,b). A characteristic feature of *K. dashzevegi* and other Mongolian multituberculates from which nearly complete, uncrushed pelves are known is that the ischiopubic symphysis is formed at an acute angle and extends ventrally as a distinct keel (Kielan-Jaworowska, 1979). As far as can be determined from available materials, North American multituberculates shared the same feature.

FEMUR

(Figures 4, 5, 7, 8, 19, 20A,B,E,F, 21)

UA 9001—The articular surface of the femoral head is slightly greater than hemispherical, more so than indicated for *Ptilodus montanus* by Gidley (1909: fig. 5). The dorsally reflected head is well set off by a cylindrical neck that joins the shaft at an angle of about 60° (Figs. 5, 8).

The robust greater trochanter extends

A
B
C
D
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A.M.N.H.
16325

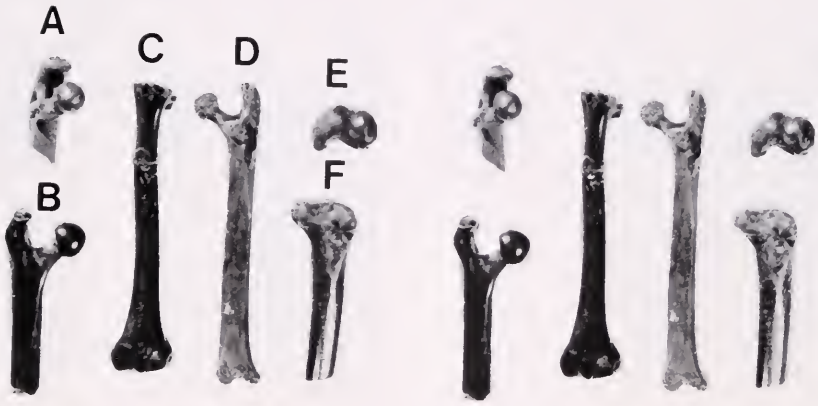

Figure 21. Stereophotographs of femora of ?*Mesodma* sp., Bug Creek Anthills locality. A) MCZ 20775, left proximal fragment, ventromedial view; B) UMVP 1423, right proximal fragment, dorsal view; C) UMVP 1424, right femur missing proximal end, dorsal view; D) MCZ 20776, right femur missing distal epiphysis, ventral view; E) MCZ 20777, left distal femur, distal view; F) MCZ 20778, right distal femur, ventral view. × 2.2.

along the axis of the shaft well above the level of the head. The expanded apex bears a large, rugose area for insertion of gluteal musculature. Distally, the insertion area is prolonged along the ventrolateral aspect of the shaft as a sharp (gluteal) crest. The digital fossa is small and narrow. The bulbous lesser trochanter, approximately one-third the size of the femoral head, projects ventrally and is a simple rounded eminence. A second fossa, between the lesser trochanter medially and the gluteal crest laterally, may be part of a divided digital fossa (Simpson and Elftman, 1928).

The shaft is circular in cross section at midlength but more elliptical proximally.

The junction between the shaft and the distal epiphysis of the femur is clearly marked. The patellar groove crosses the distal end obliquely from proximomedial to distolateral aspect and terminates dorsal to the lateral condyle. The two condyles are separated by a broad intercondyloid fossa. The facets have a large radius of curvature (i.e., are relatively flat) and are confined to the ventral aspect of the condyles. The lateral condyle, wider but less protuberant than the medial condyle, bears a shallow, round fossa adjacent to the lateral ridge of the patellar groove.

Other Material—?*Catopsalis joyneri* (UMVP 1427), left proximal fragment; ?*Cimexomys minor* (UMVP 1421), left proximal fragment; ?*Eucosmodon* sp. (AMNH 16325), complete right femur and left proximal fragment; ?*Meniscoessus robustus* (YPM 10625c), right proximal fragment; ?*Mesodma primaeva* (AMNH 77178), right proximal fragment; ?*Mesodma* sp. (UMVP 1422, 1423), right proximal fragments; ?*Mesodma* sp. (MCZ 20775), left proximal fragment; ?*Mesodma* sp. (MCZ 20776), right femur lacking distal epiphysis; ?*Mesodma* sp. (UMVP

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Figure 20. Stereophotographs of femora and fibulae of ?*Eucosmodon* sp. (AMNH 16325), San Juan Basin. A) right femur, dorsal view; B) left proximal femur, ventromedial view; C) right distal fibula, posteromedial view; D) left distal fibula, distomedial view; E) right femur, ventral view; F) left proximal femur, dorsomedial view; G) right distal fibula, anterolateral view; H) left distal fibula, distal view (top is medial). × 1.2.

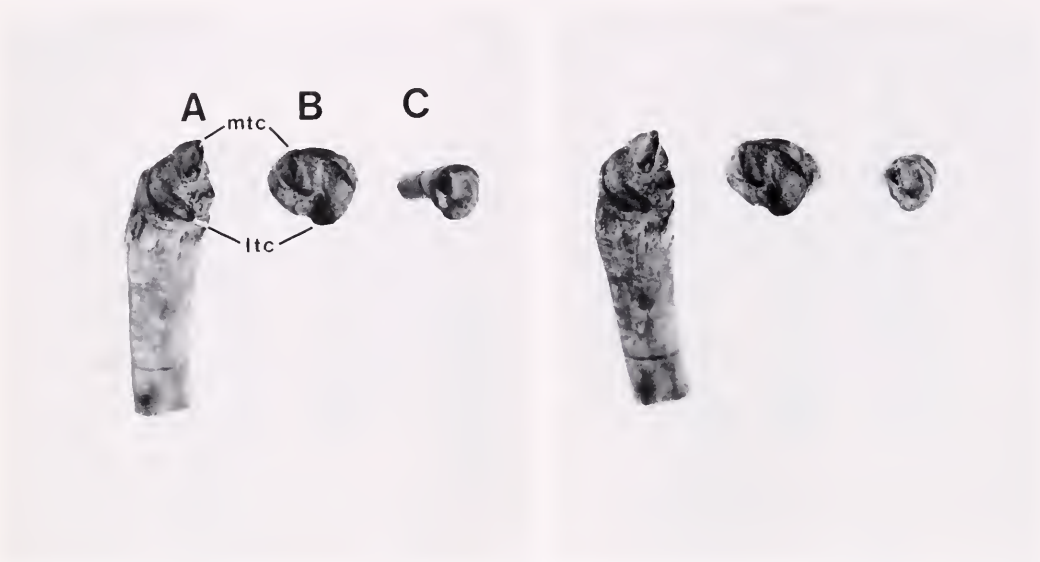

Figure 22. Stereophotographs of tibiae of North American Multituberculata. A) AMNH 16325, ?*Eucosmodon* sp., San Juan Basin, right distal fragment, posterodistal view; B) AMNH 16325, ?*Eucosmodon* sp., San Juan Basin, left distal fragment, distal view (top is anterior); C) AMNH 16024, *Stygimys teilhardi,* Torrejon Arroyo, left distal fragment, distal view (top is anterior). ×1.5.

Abbreviations: ltc, lateral tibial condyle; *mtc,* medial tibial condyle.

1424), right femur lacking head and greater trochanter; ?*Mesodma* sp. (MCZ 20777), left distal femur, and (MCZ 20778) right distal femur; ?*Ptilodus kummae* (UA 11301), left femoral head and greater trochanter; *Ptilodus montanus* (AMNH 35490), right femur lacking distal end and left femur lacking head and distal end; *P. montanus* (USNM 6076), right femur lacking distal end; ?*Stygimys kuszmauli* (UMVP 1425), right proximal fragment; ?*S. kuszmauli* (UMVP 1426), left femoral shaft; *Stygimys teilhardi* (AMNH 16024), left greater trochanter and right distal fragment.

The multituberculate femoral head exhibits a heart-shaped, somewhat flattened and slightly rugose area representing the fovea capitis femoris (Fig. 19A). The fovea, eccentrically situated on the ventral aspect of the femoral head, marks the point of attachment of the ligamentum capitis femoris.

Specimens of ?*Eucosmodon* sp. (AMNH 16325) and ?*Stygimys kuszmauli* (UMVP 1426) reveal crests running distally along the ventrolateral aspect of the shaft from the greater and lesser trochanters respectively.

The patellar groove of ?*Mesodma* sp. (UMVP 1424 and MCZ 20777) extends proximally past the epiphyseal junction and well onto the dorsal aspect of the shaft (Fig. 21C,E). The obliquity of the groove, as well as its location on the lateral side of the epiphysis, is evident in these specimens.

Patella

(Figure 7)

UA 9001—The right patella is a small, elliptical bone preserved on the lateral condyle of the tibia. Although somewhat crushed, it appears to have been concave along the articular surface, and convex along the dorsal surface.

Tibia

(Figures 4, 5, 7, 22, 23A-E, 27)

UA 9001—The proximal end is markedly asymmetric. Medially the small,

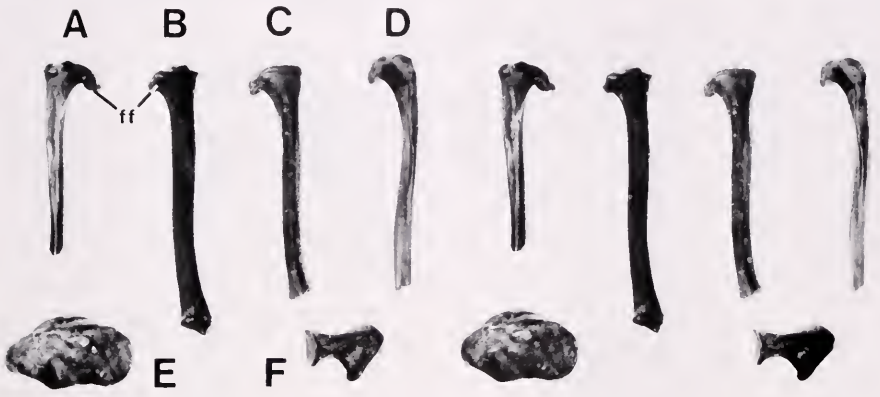

Figure 23. Stereophotographs of tibiae and parafibula of North American Multituberculata. A) MCZ 20779, ?*Mesodma* sp., Bug Creek Anthills locality, right proximal tibia, posterior view; B) UMVP 1428, ?*Mesodma* sp., Bug Creek Anthills locality, left tibia, posterior view; C) UCMP 122048, ?*Mesodma* sp., Bug Creek Anthills locality, right proximal tibia, anterior view; D) UA 11995, ?*Mesodma* sp., Bug Creek Anthills locality, left proximal tibia, posteromedial view; E) UMVP 1429, ?*Stygimys kuszmauli*, Bug Creek Anthills locality, left proximal tibia, proximal view (top is anterior); F) UA 9001, *Ptilodus kummae*, locality UAR2g, parafibula, side view (articular facet is at left, muscular process is at right; other details of this bone's orientation are unknown). × 2.2.

Abbreviations: ff, fibular facet.

slightly depressed concave facet for the medial femoral condyle is ovoid in outline; its long axis is oriented anterolaterally-posteromedially. The lateral facet is larger and its long axis is oriented transversely; the surface is saddle-shaped, convex anteroposteriorly and concave mediolaterally. The intercondyloid eminence is higher posteriorly than anteriorly. A large, hook-like flange descends distally from the posterolateral corner of the proximal end, and bears a facet on its posterior surface for the fibula. A thin lamina of bone joins the flange from the shaft of the tibia and, anteriorly, forms a shallow fossa between the two structures.

The anterior surface of the tibia is smooth and convex; there is no distinct tibial tuberosity. Posteriorly, the tibia is deeply excavated just below the proximal articular surface. The shaft bears a distinctly sigmoidal curvature; the proximal half is bowed medially, the distal half laterally.

Two condyles are developed on the distal articular surface. The long axis of the oval medial condyle is oriented anteromedially-posterolaterally; the medial extremity of the condyle forms the distal tip of the bone. The spiral lateral condyle wraps around the medial facet. The two condyles are separated by a spiral groove that accommodates an oblique ridge between the two corresponding sulci on the astragalus.

Other Material—?*Eucosmodon* sp. (AMNH 16325), proximal end of right tibia, distal ends of both tibiae; ?*Mesodma* sp. (UMVP 1428), complete left tibia; ?*Mesodma* sp. (MCZ 20779, UA 11995), right proximal fragments; ?*Stygimys kuszmauli* (UMVP 1429), right and left proximal fragments; *Stygimys teilhardi* (AMNH 16024), proximal and distal fragments; Multituberculata indet. (UMVP 6663), left tibia lacking distal end; Multituberculata indet. (UCMP 122048), right tibia lacking distal end;

Multituberculata indet. (UMVP 1641), right proximal fragment.

These tibiae reveal that the posterior fossa on the proximal end of the shaft completely undercuts much of the articular surface; the lateral articular facet and the intercondylar eminence are unsupported by bone except anteriorly. The most complete tibia (UMVP 1428) displays the characteristic sigmoidal curvature of the shaft; the proximal half is bowed medially, the distal half laterally. Features of the proximal articular surface are best exhibited on the slightly waterworn specimens of ?*Stygimys kuszmauli* (e.g., UMVP 1429). The distal end is best preserved in ?*Eucosmodon* sp. (AMNH 16325) (Fig. 22A,B).

Fibula

(Figures 4, 5, 7, 8, 20C,D,G,H, 27)

The fibula, previously poorly known in multituberculates, is preserved intact in both hind limbs of *Ptilodus kummae*. The precise orientation of the fibula, however, remains uncertain.

It appears that the large flat facet on the posterolateral margin of the tibial head articulated with a large, flat facet on the fibular head. If this interpretation is correct, the fibula was situated slightly posterior to the tibia proximally, but distally lay more lateral to it.

The left fibular head exhibits a large, convex facet along its posterior margin that articulated with the parafibula (Fig. 8). The fibular head bears a long, slender reflected process that arises from its posterolateral margin and is directed distally. Owing to the anteroposterior alignment of the proximal end of the tibia and fibula the lateral flanges of those bones were also closely aligned in an anteroposterior relationship. Both the tibial and fibular processes appear to be related to a crural musculotendinous attachment.

The shaft of the fibula is cylindrical, slender, bowed slightly posterolaterally at midlength, and expands distally to a large epiphysis. The distal epiphysis of the left fibula is separated from the diaphysis. Although the articular surfaces of both distal epiphyses are obscured by overlying bone, it is evident that the posteromedial surface is concave and articulated with a small ossicle (a ?lunula, see below) and that the lateral side is convex (Fig. 27). A tuberosity protrudes from the anterolateral margin of the epiphysis.

Although slight displacement of the articular relationships is evident, the right foot of *P. kummae* reveals that the distal end of the fibula articulated with the dorsolateral margin of the astragalus (Fig. 27).

Other Material—?*Eucosmodon* sp. (AMNH 16325), left and right distal fragments (Fig. 20C,D,G,H).

The distal end of the fibula is triangular in outline, with anterior, posteromedial, and posterolateral sides. A large, bulbous facet near the anteromedial side apparently represents the astragalar contact. A tuberosity occurs anterolaterally, and a small, prominent spine posteriorly. The distal fibula illustrated by Granger and Simpson (1929, Fig. 22C) is from the left side and is shown in posteromedial and distal views (not anterior and medial, as indicated).

Parafibula

(Figure 23F)

UA 9001—A pair of ossicles found in association with the hind limbs are here interpreted as parafibulae. Each bears a small, elliptical, concave articular surface that matches the large convex facet on the posterior surface of the proximal end of the fibula. A short, constricted neck separates the articular end from a bladelike muscular process that bears two distinct tuberosities along the margin. These parafibulae are notable for their large size.

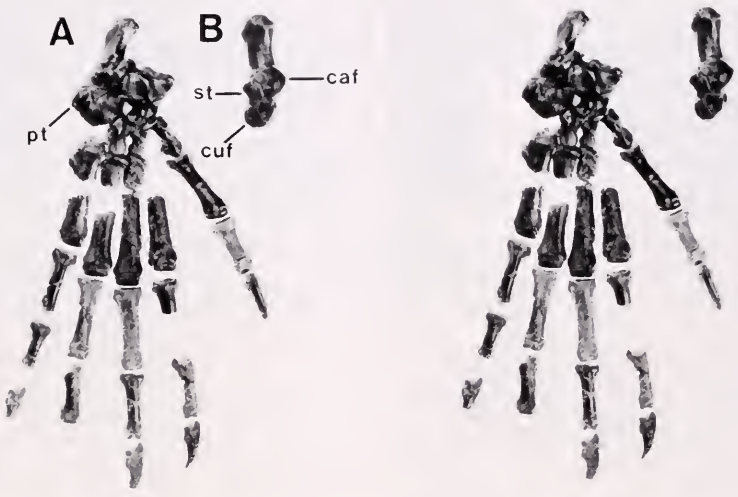

Figure 24. Stereophotographs of dorsal view of A) nearly complete right pes, and B) left calcaneum of ?*Eucosmodon* sp. (AMNH 16325). Missing from the right pes are the mesocuneiform and parts of metatarsals and phalanges of digits I–IV. Phalanges from both pedes were used to reconstruct the foot skeleton shown; their relative positions are uncertain. × 1.0.

Abbreviations: caf, proximal calcaneoastragalar facet; *cuf*, cuboid facet; *pt*, peroneal tubercle; *st*, sustentaculum tali.

Other Material—Isolated ossicles (MCZ 20806, 20807; UA 11996) from the Bug Creek Anthills locality resemble the parafibulae of *Ptilodus kummae* in basic shape, although differences exist in the tuberosities and surface features of the bladelike muscular process. A hind limb of *Kryptobaatar dashzevegi* figured by Kielan-Jaworowska (1979: fig. 1a,c) appears to have the parafibula preserved in articulation with the fibula. The ossicle, which resembles the parafibula of *P. kummae*, contacts the fibular head near its apex; the muscular process is directed dorsally (toward the extensor surface of the femur).

PES

(Figures 4, 7, 24, 25, 26, 27; Table 1)

UA 9001—The complete right tarsus is preserved almost intact; the bones of the left tarsus are disarticulated and only the calcaneum, astragalus, cuboid, navicular, ecto- and entocuneiforms can be identified with confidence.

The robust tuber calcanei, comprising the posterior half of the bone, is laterally compressed. Its posterior terminus is dorsoventrally expanded and convex in lateral profile. The bulbous proximal facet for the astragalus (astragalocalcaneal facet) is situated just medial to the midaxial line of the tuber and becomes narrower distally (a condition differing somewhat from that in ?*Eucosmodon* sp.). A low tuberosity is developed just posterolateral to the astragalocalcaneal facet. The sustentacular facet, pyriform in outline and flat, faces medially and somewhat dorsally (approximately 50° from horizontal). The sustentacular and proximal astragalocalcaneal facets are separated by a broad sulcus. A prominent peroneal tubercle protrudes distolaterally from the calcaneal body. The cuboid facet is round, slightly concave, and faces distoventromedially.

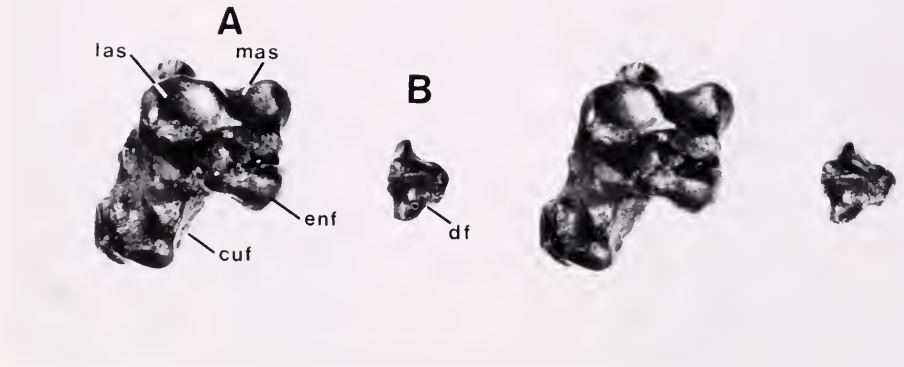

Figure 25. Stereophotographs in anterior view of A) articulated calcaneum, astragalus, and navicular, and B) entocuneiform of right pes of ?*Eucosmodon* sp. (AMNH 16325). × 2.3.

Abbreviations: cuf, cuboid facet; *df*, distal facet for metatarsal I; *enf*, navicular facet for the entocuneiform; *las*, lateral astragalar sulcus; *mas*, medial astragalar sulcus.

The dorsal surfaces of both astragali of UA 9001 are obscured by overlying bone; other features of the astragalus appear to be very similar to those of ?*Eucosmodon* sp. (Granger and Simpson, 1929: fig. 24B), and therefore it is likely that they were similar in dorsal aspect also.

The astragalus is dorsoventrally thicker medially than laterally. The calcaneoastragalar facet, situated laterally on the plantar surface of the astragalus, is concave and anteroposteriorly elongate with a marginal indentation medially. The medial half of the plantar surface is occupied by the ventrolaterally directed sustentacular facet. The astragalar foramen pierces the posterior margin of the astragalus between the calcaneoastragalar and sustentacular facets. A canal, formed by the apposition of the calcaneal sulcus and the plantar surface of the astragalus, is a continuation of the astragalar foramen. The convex naviculoastragalar facet on the prominent astragalar head passes obliquely from the lateral border in a ventromedial and then a posteroventral direction. In perpendicular section the facet is concave and thus forms a saddle-shaped joint with the navicular.

The right pes of UA 9001 preserves the navicular in approximately articulated position. The facet for the astragalus is concave. On the distal surface are two facets; one is concave and articulated directly anteriorly with the ectocuneiform and the other appears flatter and articulated with the mesocuneiform distomedially. Contact with a dorsoventrally concave facet on the cuboid distolaterally is also present.

The rectangular cuboid has well-developed facets for the ectocuneiform medially, the navicular proximomedially, metatarsal IV distally, and metatarsal V distolaterally. The facet for the calcaneum, not wholly visible, appears to be large and shallowly concave, and extends onto the dorsal aspect of the cuboid at its proximolateral corner.

The ectocuneiform is mediolaterally compressed. Both its distal and proximal facets for metatarsal III and the navicular, respectively, are dorsoventrally concave. The ectocuneiform contacts the mesocuneiform via an oval facet. Along the proximal third of the lateral surface is an elongate facet for the cuboid.

Only the dorsal aspect of the mesocuneiform, which is rectangular in outline,

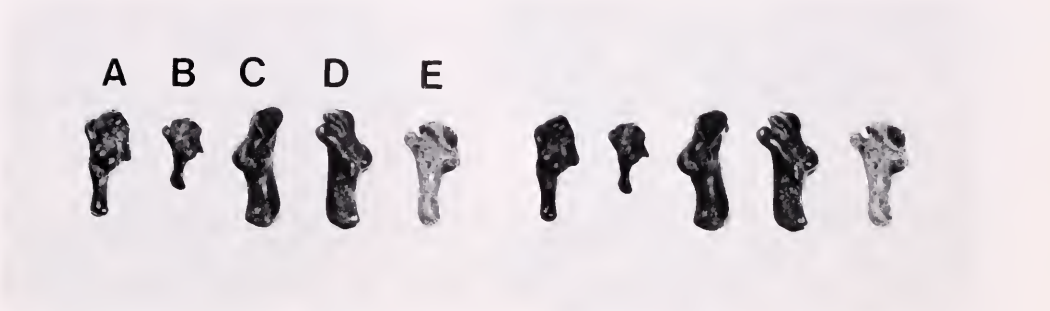

Figure 26. Stereophotographs of calcanea of North American Multituberculata. A) UA 9001, *Ptilodus kummae*, locality UAR2g, dorsal view (left); B) AMNH 77176, ?*Mesodma primaeva*, Clambank Hollow locality, dorsal view (left); C) MCZ 20782, ?*Stygimys kuszmauli*, Bug Creek Anthills locality, medial view (left); D) MCZ 20784, ?*Stygimys kuszmauli*, Bug Creek Anthills locality, lateral view (left); E) MCZ 20783, Multituberculata indet., Bug Creek Anthills locality, ventral view (right). × 1.9.

can be seen. Anteroposteriorly shorter than the ectocuneiform, it articulated with the navicular proximally, the entocuneiform medially, with metatarsal II distally (via a slightly concave facet), and with the ectocuneiform laterally.

The laterally compressed entocuneiform is the longest of the three cuneiforms. The proximal facet for the navicular is shallowly concave. The saddle-shaped distal facet for the hallucal metatarsal is concave dorsoventrally and convex transversely. The ventral projection of the distal facet is narrower and more slender than the dorsal projection. Granger and Simpson (1929: fig. 23) reconstructed the pes of ?*Eucosmodon* with the narrow ventral lip of the entocuneiform in a dorsal rather than plantar position. The pes of *Ptilodus kummae* clearly shows that the narrow lip of the entocuneiform is ventral in position.

Preserved with the right tarsus of UA 9001 are two problematical ossicles. One probably articulated via a convex facet with the proximal terminus of the entocuneiform and its position indicates that it is probably a tibiale (Fig. 27A). Its other articulations are uncertain but contact with the navicular laterally, and perhaps also with the astragalus proximally, is possible. In a review of the homologies of the tibiale, Lewis (1964) pointed out that in monotremes the tibiale articulates proximally and laterally with the astragalus and distally with the navicular. The oblique orientation of the navicular in UA 9001 provides potential space for the tibiale to have also articulated with the entocuneiform.

A second problematical ossicle is preserved in tight articulation with the distal articular surface of the fibula (Fig. 27B). Only the medial surface of the bone can be seen; it is oval in outline and quite small. It is probably not a sesamoid bone because of its position on the medial side of the distal end of the fibula. More than two tarsalia in the proximal row are unknown among mammals. Early workers (see review by Lewis, 1964) reported the occurrence of a third proximal bone (the intermedium tarsi) in pedes of several marsupials as well as in humans (the os trigonum, thought to represent the intermedium tarsi). Lewis (1964: 207) concluded, however, "that the so-called marsupial intermedium is merely a lunula within an inter-articular meniscus" and that "there is . . . little reason for regarding the anomalous human os trigonum as an intermedium tarsi. Perhaps it is not even the homologue of the marsupial lunula, and nothing more than an aberrant ossification of no morphological significance." Although the evidence is unclear, the ossicle

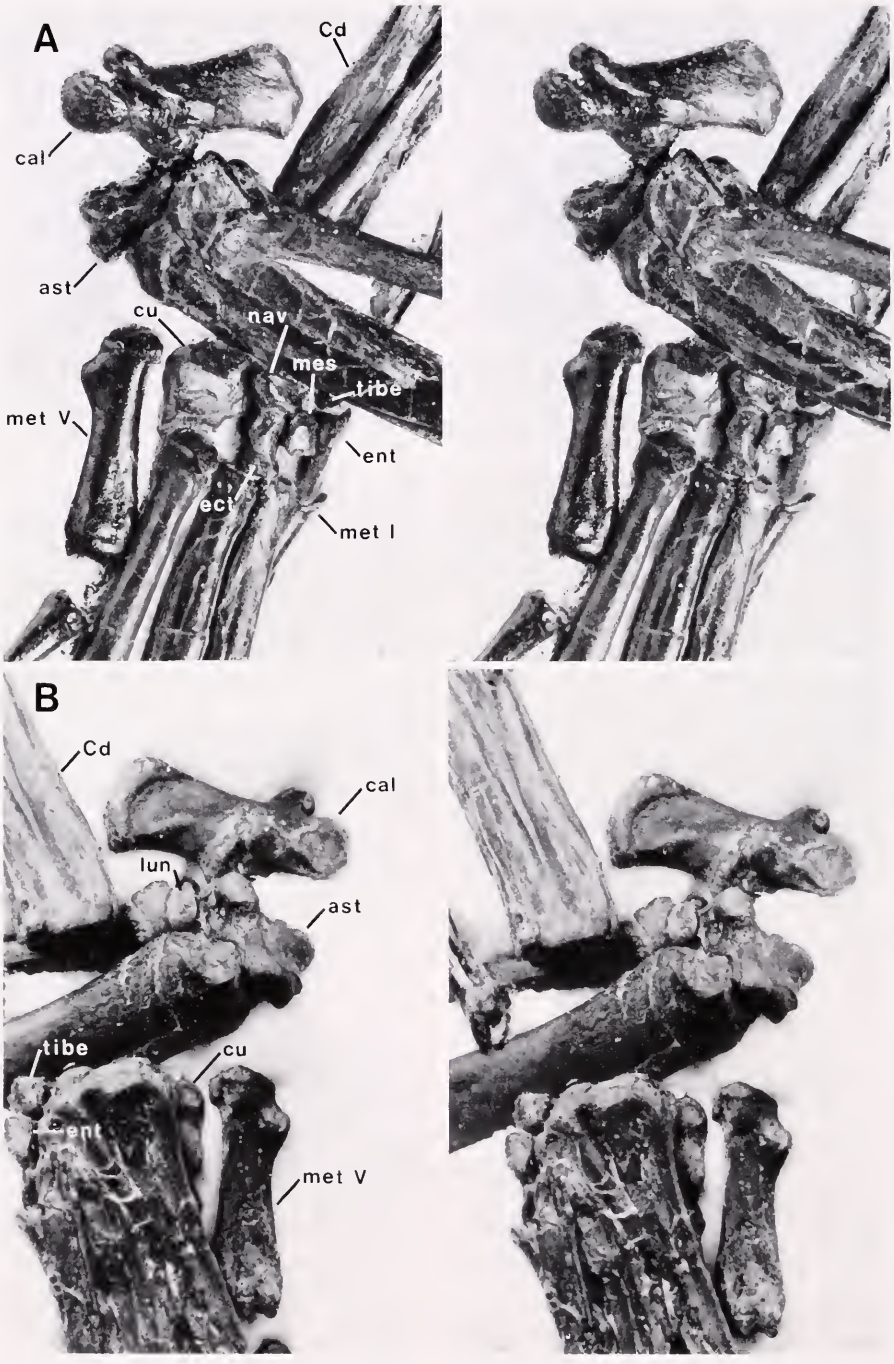

Figure 27. Stereophotographs of the right pes of *Ptilodus kummae* (UA 9001) in A) dorsal and B) ventral views. × 4.3.

Abbreviations: ast, astragalus; *cal*, calcaneum; *Cd*, caudal vertebra; *cu*, cuboid; *ect*, ectocuneiform; *ent*, entocuneiform; *lun*, lunula; *mes*, mesocuneiform; *met I, V*, first and fifth metatarsals; *nav*, navicular; *tibe*, tibiale.

TABLE 1. LIMB MEASUREMENTS (mm.) OF UA 9001 (*Ptilodus kummae*).

Digit	I	II	III	IV	V	
Metatarsal length	6.9*	10.4	11.8	11.2	7.8	
Proximal phalanx length	—	6.4	6.2	6.3	4.5	
Middle phalanx length	—	5.7	5.7	5.5	3.8	
Distal phalanx length	3.3	3.6	3.4	3.5	3.3	
Length of right femur						36.4
Length of left femur						36.0
Length of right tibia						28.8
Length of right fibula						25.4
Length of right ilium (from anterior rim of acetabulum to anterior tip)						28.4

* Approximate.

associated with the distal fibula of *P. kummae* is here interpreted to be a lunula.

The relative lengths of the metatarsals are III > IV > II > V > I.

The proximal articular facet of the hallucal metatarsal is saddle-shaped (dorsoventrally convex, transversely concave). The distally directed ventral lip of the entocuneiform lies between two proximoventrally directed processes of the hallucal metatarsal, the medial one of which is larger. The shaft of metatarsal I, as in all the metatarsals, is somewhat dorsoventrally compressed. The distal articular surface cannot be seen.

Metatarsals II, III, and IV are basically similar except in length and in the shape of the proximal bases, which become progressively wider from II to IV. Metatarsal V bears a prominent, rounded lateral projection just distal to the proximal facet where a peroneal or short abductor tendon may have inserted. The proximal articular surfaces of metatarsals II to IV are dorsoventrally convex; that of metatarsal V is a flat, dorsoventrally elongate facet on the proximomedial corner of the bone.

An oblique groove between the apposed medial side of metatarsal III and the lateral side of metatarsal II, just distal to the proximal bases, probably provided passage for a perforating metatarsal artery from the dorsal to the plantar aspect of the hind foot.

Two oval plantar sesamoids are associated with the distal ends of metatarsals IV (left pes) and V (right pes), whereas a conjoined one is present on metatarsal II (left pes).

Pedal phalanges of all ten digits are preserved. The proximal and middle phalanges of the digits are all similar except in length (Table 1), and are of a typically mammalian pattern. The proximal articular surfaces of proximal phalanges are concave. The distal articular ends of the proximal phalanges (except I) are well-rounded dorsoventrally and only slightly convex in a transverse plane; those of the middle phalanges and proximal hallucal phalanx have a prominent trochlea to accommodate the distal phalanges. The shaft of each proximal and distal phalanx tapers distally and is elliptical in cross section. Several plantar sesamoids are associated with the phalanges of both pedes.

Distal phalanges of the pes are similar in structure to those of the manus but are considerably more elongate.

Other Material—?*Eucosmodon* sp. (AMNH 16325), nearly complete right and left pedes; ?*Cimexomys minor* (UMVP 1430), left calcaneum; ?*Meniscoessus major* (AMNH 77264), left calcaneum; ?*Mesodma* sp. (UMVP 1432), right calcaneum; ?*Mesodma primaeva* (AMNH 77176), left calcaneum; ?*Stygimys kuszmauli* (UMVP 1433), right calcaneum; ?*S. kuszmauli* (MCZ 20792, MCZ 20784), left calcanea; Multituberculata indet. (PU 14487), left calcaneum; Multituberculata indet. (MCZ 20783), right calcaneum; Multituberculata indet. (UM 72711), left astragalus.

The hind feet of ?*Eucosmodon* sp. (AMNH 16325), first described by Granger and Simpson (1929), represent the best available material for interpreting the posture and movements of a multituberculate foot. The right foot appears to lack only the mesocuneiform and various phalanges (the ectocuneiform is present, contrary to Granger and Simpson, 1929). The left foot lacks the astragalus, entocuneiform, metatarsal I, and some phalanges. It is unnecessary to recapitulate Granger and Simpson's morphological description, except to note that in their Figure 23 the entocuneiform is upside down and the hallux is depicted in a relatively adducted posture. The articular surfaces indicate that in the neutral position the hallux was divergent, probably on the order of 30° from the axis of metatarsal III.

Marsh (1889) described a calcaneum and an astragalus (YPM 10639) that he believed were from a multituberculate. Although doubts have been cast on the identity of other postcranial bones that Marsh referred at the same time to the Multituberculata (see above), McKenna (1961) agreed with Marsh's allocation of the two tarsals. Our opinion is that the calcaneum could well be that of a multituberculate, but in several features (e.g., the vestigial nature of the sustentaculum) it is unlike any other multituberculate. The astragalus is very different from that of *Ptilodus* and ?*Eucosmodon*.

OSTEOLOGY OF THE POSTCRANIAL AXIAL SKELETON

Thoracic Series
(Figures 3, 6)

UA 9001—At least six and possibly seven posterior thoracic vertebrae are preserved in UA 9001; none of the anterior thoracics or cervical vertebrae were recovered. The preserved thoracic vertebrae are variously disarticulated, crushed, and fragmented.

The centra in the posterior part of the thoracic series are compressed dorsoventrally. The anterior end of each centrum is transversely elongate; the ventral half of the articular surface is recessed, and the dorsal half bulbous. The posterior articular end is almost circular in outline, except for a slight dorsal flattening, and is shallowly concave. The sides of the anterior end extend as lips to accommodate the rounded lateral margins of the preceding centrum. Below the lip, on the ventrolateral margin of the anterior end, is a costal facet for the rib head. On one of the more posterior thoracic vertebrae, a costal facet appears to have been developed on the ventrolateral margin of the posterior end, and thus the capitular articulation was intervertebral. Two shallow fossae, separated by a median crest, mark the ventral surface of each of the thoracic centra.

The pedicles are shorter than the laminae and the vertebral canal is consequently transversely elliptical. Low circular diapophyses are situated near the anterior margin of the pedicles. On the more anterior thoracics, they are protuberant and dorsally situated; on the posterior thoracics, diapophyses are developed on the pedicle-centrum junction. Stout anapophyses project caudad from the posterior margins of the pedicles.

Spinous processes in the posterior thoracic series and anterior lumbar series are triangular in cross section, the acute-angled apex of the triangle being situated along the anteroventral margin. These processes were of low enough inclination to lie between the posterodorsally directed postzygapophyses of the preceding vertebra. The precise position of the anticlinal vertebra cannot be determined. One thoracic vertebra has a spinous process which, although comminuted, appears to be in place and is more or less vertical. Two other thoracic vertebrae (assuming seven lumbars), exhibit evidence of anteriorly inclined spinous processes. The anticlinal vertebra must therefore have been located anterior to the penultimate thoracic.

Figure 28. Stereophotographs of lumbar vertebrae of ?*Eucosmodon* sp. (AMNH 16325) in A) anterior, B) right lateral, and C) dorsal (anterior is to left) views. × 1.0.

The zygapophyses are robust and protuberant; the concave prezygapophyseal facets face dorsomedially, the convex postzygapophyseal facets ventrolaterally. Low ridges, one passing anteriorly from the dorsal aspect of each postzygapophysis, converge along the dorsolateral margins of the neural spine, and meet at the spine's distal terminus.

LUMBAR SERIES

(Figures 4, 5, 7, 8, 28; Table 2)

UA 9001—At least seven and possibly eight lumbar vertebrae are preserved; the last six are articulated. The thoracolumbar transition cannot be determined because of postmortem damage.

The centra of anterior lumbar vertebrae are wider than deep, as in posterior thoracics. Posteriorly the lumbar centra appear to become increasingly longer and wider, with the exception of the last lumbar, which is shorter but wider than L6 (L7?). Transverse processes extend anteroventrolaterally and become longer and broader toward the sacrum. The transverse processes of the last lumbar, however, are laterally directed.

Midventral keels are larger on anterior lumbar vertebrae than on the posterior thoracics. They appear to be absent on the posterior lumbar vertebrae. From anterior to posterior the spinous processes of the lumbars become more slender and more erect although an anterodorsal inclination is maintained. The zygapophyses become more robust and more widely spaced toward the sacrum.

Other Material—?*Eucosmodon* sp. (AMNH 16325), three nearly complete lumbar vertebrae; *Stygimys teilhardi* (AMNH 16024), three lumbar centra.

The spinous processes on the lumbar vertebrae of ?*Eucosmodon* sp. (AMNH 16325) (Fig. 28) are more or less vertical and, in one, the spinous process appears to be inclined slightly posteriorly (Granger and Simpson, 1929). This feature, as well as the well-developed transverse processes, indicate that the lumbar vertebrae preserved in this specimen are probably well posterior in the series. The centra are approximately circular in cross section.

SACRAL SERIES

(Figures 5, 8)

UA 9001—The first sacral vertebra is slightly shorter than the last lumbar and bears robust transverse processes that are directed laterally and slightly posteriorly. The anterior half of the terminus expands to form an articular facet for the ilium; the thin, emarginated posterior half is apparently nonarticular. The posterior end

TABLE 2. VERTEBRAL MEASUREMENTS (mm.) OF UA 9001 (*Ptilodus kummae*).

Vertebra	Length pre- to postzyga	Length centrum	Width prezyga	Width postzyga.	Width tr. processes
L1 (L2?)	7.3	—	5.4	4.4	7.1*
L2 (L3?)	8.0	—	5.7*	4.4*	8.8*
L3 (L4?)	—	—	—	4.7*	10.4*
L4 (L5?)	8.2*	—	6.1*	5.1*	—
L5 (L6?)	8.3*	—	6.2*	5.8*	13.6*
L6 (L7?)	—	—	—	—	14.9*
L7 (L8?)	—	—	—	6.2*	19.0*
S2	—	—	—	—	9.3*
Cd1	—	3.9*	—	—	8.6*
Cd2	6.2	—	5.6	4.5	—
Cd3	6.3	—	5.7	4.2	10.8*
Cd4	6.5	—	5.6	3.9*	—
Cd5	7.8	—	—	—	9.9*
Cd6	—	8.5*	—	—	9.4*
Cd7	—	10.7	—	—	8.0*
Cd8	—	11.0*	—	—	—
Cd9	—	11.2*	—	—	—
Cd10	—	11.4*	—	—	—
Cd18?	—	6.9	—	—	—
Cd19?	—	6.2	—	—	—
Cd20?	—	5.7	—	—	—
Cd21?	—	5.0	—	—	—
Cd22?	—	4.1	—	—	—
Cd23?	—	3.4	—	—	—
Cd24?	—	2.9*	—	—	—

* Approximate.

of the centrum is expanded transversely, but is not synostosed with the centrum of S2.

The second sacral vertebra is firmly synostosed with S3. The transverse processes of S2 are oriented anterolaterally. A prominent pair of ventral foramina occur on the ventral surface of the S2 centrum.

The suture between S2 and S3 is not visible. As preserved, most of S3 and its articulation with the next posterior centrum are obscured ventrally by the proximal end of the left femur. Dorsally, it appears that the centrum of S3 is fully fused with the next posterior one, indicating that the specimen has four sacral vertebrae.

At least on S3 and S4 the neural spines are prominent and erect. The centrum of S4 is elongate and relatively narrow transversely; the distal extremities of the transverse processes are missing. A large nutrient foramen occurs on the ventral surface just posterior to the middle. Several foramina are present in the transverse processes of S4, but do not appear to be developed in other sacrals. A fragmentary haemal arch is preserved in articulation with the posteroventral margin of the centrum of S4. The distal part of the arch is broken away.

Other Material—Stygimys teilhardi (AMNH 16024), sacral fragment consisting of parts of two fused vertebrae (S1? and S2?).

CAUDAL SERIES

(Figures 3-8; Table 2)

UA 9001—P. kummae possesses at least five, and probably six, anterior caudal vertebrae (*sensu* Lessertisseur and Saban, 1967).

The transverse processes of Cd1 to Cd5

arise from almost the entire length of the centra and are directed anterolaterally (Figs. 5, 8). On succeeding caudal vertebrae transverse processes become progressively smaller and more laterally oriented. A foramen pierces the posterior base of each transverse process of the anterior caudals.

The centrum of Cd1 is only slightly longer than wide. The remaining anterior caudal vertebrae become progressively longer, the largest increase occurring from Cd4 to Cd5 (Table 2). The zygapophyses of Cd1 to Cd4 are large; on Cd5 they are small and on Cd6 the prezygapophyses are much reduced and the postzygapophyses rudimentary. The prezygapophyseal facets of the anterior caudals are saddle-shaped, that is, convex anteroposteriorly and concave transversely. As a whole, they are posteriorly inclined at a small angle to the horizontal. The spinous processes of Cd1 to Cd4 are erect, centrally located, and decrease progressively in height posteriorly such that the process of Cd5 appears to be an elongate, low, sagittal crest (it may, however, be broken).

The haemal arches ventral to the anterior caudal vertebrae are relatively large. The haemal canals are triangular, the apices being directed ventrally. The spinous processes ventral to the canals are laterally compressed, spatulate in side view, and nearly perpendicular to the centra in orientation. Further posteriorly, the spinous processes become progressively less perpendicular, projecting anteroventrally until, at about Cd10, they are nearly parallel to the centra. The haemal spine between Cd6 and Cd7 differs from those described above in being dorsoventrally rather than laterally compressed; the distal end is evenly rounded.

The proximal posterior caudal vertebrae (Cd6–Cd10) (an anterior fragment of Cd11 is also present) increase in length posteriorly, that is, the longest caudal vertebra is Cd10 or is posterior to Cd10. Cd7 to Cd10 bear anterior paired mammillary processes, transverse processes, a low, elongate spinous process, and paired anteroventral processes for articulation with the haemal arches. All these features decrease in size posteriorly. The centra are elongate and cylindrical, expanding slightly at their extremities. The haemal spines posterior to Cd7 are dorsoventrally compressed and bear a sagittal, U-shaped notch on the distal end, rather than being evenly rounded as on Cd6.

The positions of the three caudal vertebrae recovered by washing and screening are uncertain. However, for ease of reference, these vertebrae are tentatively identified as Cd16, Cd18, and Cd19. The processes and crests observed on Cd7 to Cd10 are only slightly developed on these caudals. In lateral view, the centra are dorsally concave and ventrally convex.

The end of the tail is preserved in UA 9001 and the individual centra are tentatively identified as Cd20 to Cd26 (Figs. 3, 6). Haemal arches on Cd20 to Cd24 are slender structures that lie parallel to and beneath the centra. Each is incised with V-shaped notches proximally and distally, the latter being the deeper.

The length of the tail can be estimated with some confidence. Twenty-one complete or partial caudal vertebrae were recovered. In view of the disparity in lengths between the articulated tenth caudal vertebra and the distal caudals (Table 2), we estimate that the tail had at least 24 and possibly as many as 28 vertebrae. The sum total of the measured and estimated lengths of the 21 known vertebrae is approximately 130 mm. Cd10 is 11.4 mm in length, and the next distal caudal preserved (Cd16?) is a disarticulated specimen that, although one end is broken, could have been no longer than 8.5 mm. Assuming a relatively large gradational length change of 1 mm, the total length of the tail would have been 150 mm with 23 vertebrae. However, gradational length changes in the two "articulated" series of posterior caudal vertebrae are less than 1 mm. It is likely, therefore, that at least three vertebrae are missing, and that minimum tail length was about 160 mm. Given the gradual increase in length in the

Cd6–Cd10 series, and assuming the unlikelihood of an abrupt reversal in gradient, the tail may be estimated to have been 180 mm or more in length.

Other Material—?*Eucosmodon* sp. (AMNH 16325), one anterior and four or five posterior caudal vertebrae, plus many fragments; *Stygimys teilhardi* (AMNH 16024), numerous fragments of caudal centra.

Like those of *Ptilodus kummae*, the known caudal vertebrae of ?*Eucosmodon* sp. and *Stygimys teilhardi* are large and robust, and indicate rather long and heavy tails.

Ribs

(Figures 3, 6)

UA 9001—Fragments of at least fifteen ribs, belonging to both left and right sides, are preserved. Several ribs are nearly complete and well preserved. On anterior ribs, the head is separated from the tubercle by a neck; the articular facet of the head is crescentic in outline, whereas the tubercular facet is larger and circular. The rib shafts are elliptical in cross section.

FUNCTIONAL ANATOMY

The postcranial skeleton of multituberculates possesses a number of unusual and even unique features. These include a scapulocoracoid with a reduced coracoid but without a supraspinous fossa, an enlarged prepollex, a dorsally emarginate acetabulum, a postobturator foramen within the ischiopubic symphysis, a large parafibula, a slender, ventrally directed lateral flange on the proximal end of the fibula, a deep excavation posteriorly beneath the proximal articular surface of the tibia, the structure of the tarsus and particularly that of the astragalus and calcaneum, and thoracic centra in which the anterior epiphysial surface is recessed ventrally and bulbous dorsally.

In this section we attempt to assess those features that may be interpreted by comparison with analogous conditions in other mammals. The functional significance of many features, however, remains open to speculation for lack of adequate comparative or experimental data.

Shoulder

The scapulocoracoid of multituberculates is well advanced beyond that in morganucodontids (Jenkins and Weijs, 1979). The coracoid is reduced to a beak-like process and would not have restricted the excursion of the shoulder by virtue of a sternal articulation (as is the case in monotremes, and possibly in morganucodontids). The glenoid fossa is directed largely inferiorly as in advanced mammals. Furthermore, the glenoid appears to be relatively small.

The relative size and shape of the glenoid and humeral head are the critical features for reconstructing excursions at the glenohumeral joint. Unfortunately, an associated scapulocoracoid and humerus are unknown for any North American multituberculate, and even proximal humeri are rare (despite abundant distal humeri in collections from the Bug Creek Anthills locality). The humeral head of *Ptilodus montanus* (USNM 6076) is damaged and broken from the shaft (Fig. 11H,I) and cannot be reconstructed accurately. However, another proximal humerus that we have tentatively identified as ?*Ptilodus montanus* (USNM 9735; Fig. 11A,B,C) is basically similar to that of *Tugrigbaatar saichanensis* from the Late Cretaceous of Mongolia (Kielan-Jaworowska and Dashzeveg, 1978). The head in both is hemispheroidal and reflected dorsally. Kielan-Jaworowska and Dashzeveg (1978: 124) note that "other, undescribed multituberculate humeri from Mongolia in the (Zakład Paleobiologii) collection, belonging to the genera ?*Kryptobaatar* and *Chulsanbaatar*, show similar prominence of the head." These findings contrast to Simpson's (1928a) reconstruction of the humeral head of *Catopsalis matthewi* (AMNH 20440, also from the Late Cre-

taceous of Mongolia), which depicts a relatively flat head more or less centered on the proximal end and not reflected dorsally. However, our reexamination of the specimen reveals that the margin of the head adjoining the dorsal (extensor) surface of the shaft has been lost. Were the missing part present, the humeral head of *C. matthewi* would resemble the pattern known from other multituberculates.

Thus, on present evidence, multituberculates appear to have had considerable disparity in size between the glenoid and bulbous humeral head, indicating ". . . the possibility of extensive flexibility of movements of the forelimb upon the scapula" (Clemens and Kielan-Jaworowska, 1979: 117). Our assessment is that multituberculate shoulder posture and mobility were comparable to those of modern therians.

Jenkins and Weijs (1979) have suggested that the anterior surface of the large scapular spine of multituberculates may have served as the origin of a muscle equivalent to the supraspinatus. Such a reconstruction is consistent with the hypothesized mobility of the shoulder, for the supraspinatus, infraspinatus, and subscapularis are the primary muscles responsible for the integrity of the mammalian glenohumeral joint which otherwise has little structural stability.

Elbow

Jenkins (1973) suggested that the spiral, condylar form of the multituberculate humero-ulnar joint allowed the forearm to extend in a sagittal plane as the humerus underwent rotation, adduction, and retraction during the propulsive phase. Inasmuch as similar excursions are accommodated by the spiral, trochlear humero-ulnar joint of primitive therians, the significance of the difference between the condylar and trochlear joint types is unclear. It is known that the trochlear type virtually restricts humero-ulnar movement to flexion-extension. Sloan and Van Valen (1965: 222) asserted that ulnar movements in multituberculates were "restricted to a single plane by the shapes of the trochlea and semilunar notch" (see also Van Valen and Sloan, 1966). In order to demonstrate this, however, a detailed analysis of the joint surfaces of an *associated* humerus, ulna, and radius must be undertaken. It seems more likely that the condylar humero-ulnar joint may have provided for a second degree of freedom (rotation), a movement that Recent monotremes probably employ with a similar type of joint.

The bulbous capitulum and the sphericity of the proximal articular surface of the radius are evidence that multituberculates were capable of pronation-supination. The fact that the proximal radial facet for the ulna extends some 90° around the head indicates this capability to have been substantial.

Manus

A sesamoid on the radial side of the wrist (usually between the scaphoid and trapezium) occurs commonly in mammals (von Bardeleben, 1894; Davis, 1964). Usually small in size (as in primates, procyonids, and ursids), the radial sesamoid is associated with various muscles (e.g., the tendon of the abductor pollicis longus in dogs; Evans and Christensen, 1979; the palmaris longus, abductor pollicis brevis and longus, and opponens pollicis of *Ailuropoda*; Davis, 1964). In certain taxa, however, the radial sesamoid is enlarged to serve specialized functions of the manus and is referred to as a prepollex. An enlarged prepollex anchors the patagium in flying squirrels (*Petaurista*), augments the fossorial capabilities of talpids (e.g., *Talpa*) and lemmings (*Lemmus, Dicrostonyx*), and provides additional prehension in some carnivores (e.g., *Ailuropoda, Potos*). The prepollex of *Ptilodus kummae* is slightly over half the length of the pollical metacarpal, and is large enough to have extended the palmar grip.

The pollex of *P. kummae*, although divergent, appears to have been limited in its movement largely to flexion-extension.

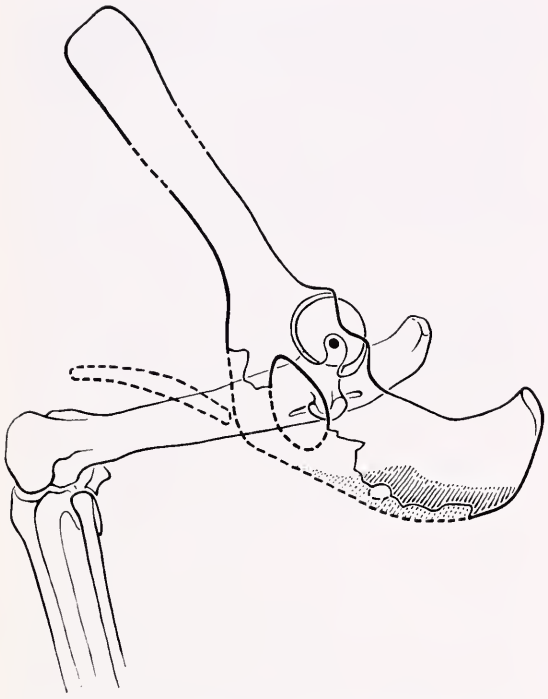

Figure 29. A reconstruction of the pelvis and hip in ?*Eucosmodon* sp. (based principally on AMNH 16325) showing the relation of the fovea capitis femoris (black dot) within the acetabular fossa. The right pelvis is rendered from medial aspect and as if it were transparent. Dark cross-hatching indicates the known extent of the pelvic symphysis; light cross-hatching represents reconstructed symphysial area. Note that the dorsal margin of a postobturator foramen is present. × 1.1.

The pollical carpo-metacarpal joint is not saddle-shaped. The proximal surface of metacarpal I is broad and articulated with flat facets on the distal surfaces of the trapezium and trapezoid and the proximomedial surface of metacarpal II.

Pelvis and Hip

Van Valen and Sloan (1966: 276) cited a "dorsally open" acetabulum among the several postcranial features of multituberculates that they hypothesized to be inferior to the therian condition. They concluded that the femur must have been "held in articulation only by muscles in this direction. This suggests a near or complete lack of ricochetal or gliding habits among multituberculates and may have permitted at most only a low possibility of arboreal activity." Our assessment of this feature is different. A number of therian joints, most notably the glenohumeral, rely largely on muscles for stabilization; those that function in this manner are typically highly mobile. It is possible, therefore, that the absence of bone around the dorsal aspect of the multituberculate acetabulum provided for an unusual degree of femoral mobility, particularly in abduction. Elftman (1929) noted that in certain arboreal marsupials, most notably in the gliding phalanger *Petauroides*, the dorsal margin of the acetabulum is incised to facilitate femoral abduction. We think it likely that at least part of the dorsal "hiatus" of multituberculates was closed by fibrocartilaginous tissue such as typically occurs in mammals (the acetabular labrum) and bridged the acetabular notch as the transverse ligament. Thus reconstructed, multituberculates possessed a relatively shallow acetabulum, indicative of highly mobile hind limbs (see Jenkins and Camazine, 1977).

The position of the fovea capitis femoris on the femoral head indicates that multituberculates employed an abducted femoral posture. The fovea represents the point of attachment of the ligamentum capitis femoris which is confined within the acetabular fossa; displacements of the fovea observed in various mammals are related to differences in femoral posture and excursion (Jenkins and Camazine, 1977). In multituberculates, the fovea is located on the ventral (flexor) side of the head. Assuming that the acetabulum and acetabular fossa are aligned more or less in a sagittal plane, such a location of the fovea requires that the femur be considerably abducted (Fig. 29). In a neutral posture the long axis of the femur is estimated by this method to lie at about 45° to the median plane.

The postobturator foramen, unknown in any other order of mammals, is open

to speculation in terms of its function. The lateral surface of the ischium in mammals is typically the site of origin of muscles that adduct or externally rotate the femur. The postobturator foramen is located within the symphysis along the ventral margin of the ischium; it does not communicate with the pelvic cavity. In this region it is logical to reconstruct the attachment of femoral adductors. In comparison with the pelvis of other mammals, the multituberculate ischium presents an unusually broad area for muscle attachment. It is possible that the stress of opposing adductors along the ventral margin of the ischium is responsible for the fenestration. A functionally analogous situation may be with the true obturator foramen where the obturator externus and internus act from opposite sides of a common membrane.

Kielan-Jaworowska (1979) analyzed the possible relationship between pelvic structure and reproduction in a Cretaceous multituberculate (*Kryptobaatar dashzevegi*) from Mongolia. Noting the overall relative narrowness of the pelvis, the acute angle of intersection between the two sides, and the extensive fusion along the keel-like ischiopubic symphysis, she calculated the dimensions of the pelvic outlet which led her to the conclusion that multituberculates were viviparous and had extremely small neonates.

KNEE

Femoral condyles of multituberculates are confined to the inferior (flexor) aspect of the bone, and do not extend around the distal extremity to be contiguous with the patellar groove. From this evidence, multituberculates employed the crouched posture characteristic of primitive mammals and appear to have been incapable of extending the knee much beyond 120°. The orientation of the center of the femoral condyles indicates that the tibia, in the middle of its range of excursion, articulated with the femur at about 90°.

The asymmetry of the femoral condyles and the eccentricity of the patellar groove in multituberculates is similar to that in morganucodontids and certain primitive therians (Jenkins and Parrington, 1976). The possibility that joints of this type are adapted to accommodate some rotation at the knee during the propulsive phase remains to be investigated.

The parafibulae of *Ptilodus kummae* are relatively large. Parafibulae are found in various marsupials and rarely in eutherians; in monotremes they occur as prominent, broad flanges synostosed to the proximal end of the fibulae and in *Ornithorhynchus*, at least, provide attachment for the long digital flexor, long peroneal, soleus, plantaris, and peroneal flexor muscles (Lessertisseur and Saban, 1967). In size and shape the parafibulae of *P. kummae* resemble more closely those of monotremes than the ill-defined ossicles found in therians. Unlike the monotreme conditions, however, they articulate with the fibula via a synovial joint. The possible homologies of the parafibulae, as well as the functional implications of their presence or absence, are not well understood (for a discussion, see Lessertisseur and Saban, 1967).

PES

The tibio-astragalar and astragalocalcaneal joint surfaces in all the multituberculate specimens available for this study exhibit the same basic features, and are indicative of an unusual range of pedal movements that are typically employed by mammals that climb.

The tibio-astragalar joint not only appears to have allowed dorsiflexion and plantarflexion, but abduction and eversion as well. The dorsal (proximal) surface of the astragalus bears two subparallel sulci, one medial and the other lateral (Fig. 25). The sulci are approximately aligned with the hallux (Fig. 24A) and received the medial and lateral condyles on the distal end of the tibia (Figs. 22, $30A_2$). Some

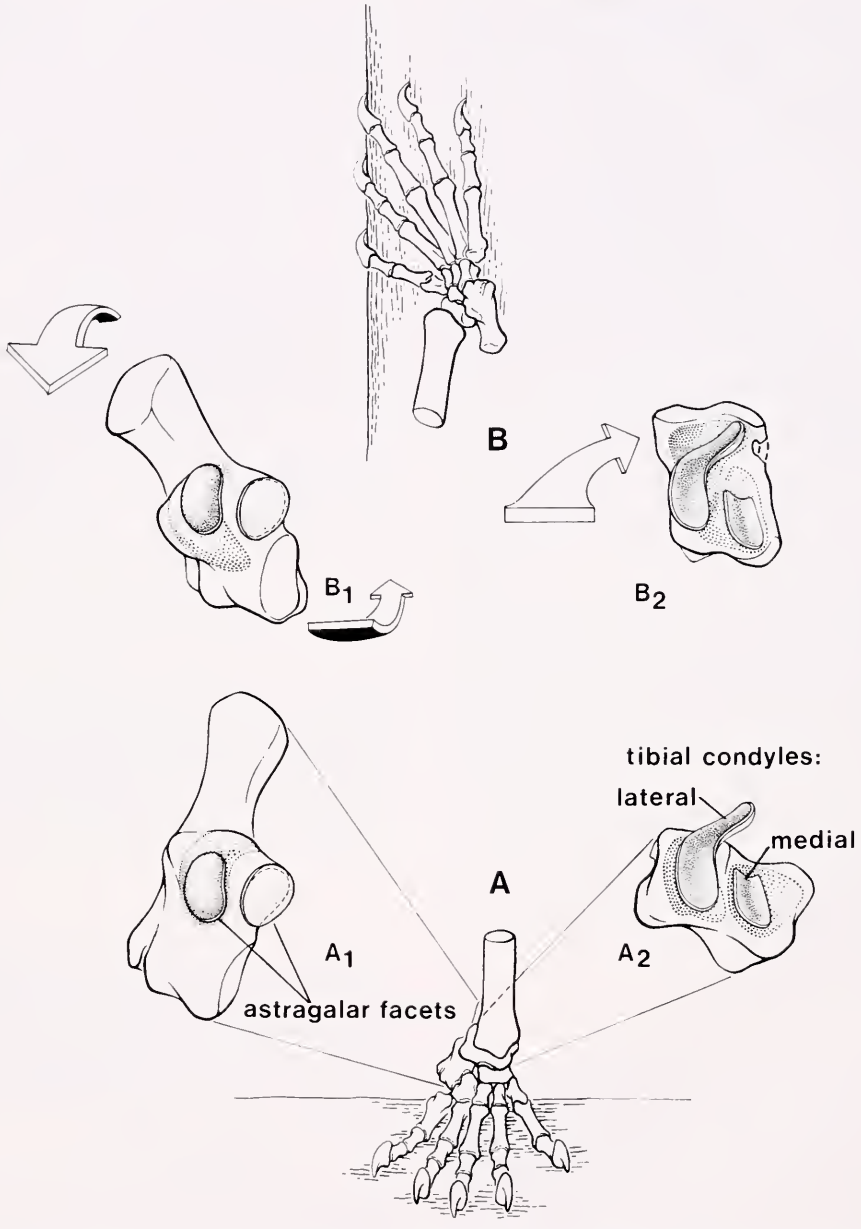

Figure 30. Tarsal movements in a multituberculate foot, interpreted from the pedes of ?*Eucosmodon* sp. (AMNH 16325) and *Ptilodus kummae* (UA 9001), that position the foot to secure a grip during headfirst descent. (A) the neutral position: the relations of the astragalar facets to the calcaneum (A_1) and the relations of the tibial condyles to the astragalar sulci (A_2) are shown. (B) The reoriented position: rotation at the astragalocalcaneal joint (B_1) yields plantarflexion and inversion. Rotation at the tibio-astragalar joint (B_2) yields abduction and eversion. Additional adjustments permitting inversion-eversion and dorsiflexion-plantarflexion are possible at the astragalonavicular and calcaneocuboid joints. The reoriented position of the foot also requires extension at the hip joint, thus repositioning the tibia and fibula nearly parallel to the substrate in (B), in contrast to the nearly perpendicular orientation in (A). The fibula is not shown.

plantarflexion and dorsiflexion could have been effected by the astragalar sulci rocking backwards and forwards across the most distal surfaces of the tibial condyles. Additional plantarflexion and dorsiflexion were possible at the astragalocalcaneal joints (Figs. $30A_1$, B_1).

Abduction and related movements suitable for securing grips over a wide range of foot postures appear to have been accommodated by the asymmetrical configuration of the tibial condyles. The lateral condyle is longer than the medial, and wraps spirally around the distal end of the tibia from its anteromedian to posteromedian margins (Fig. 22). The short, linear medial condyle extends from the anterior margin to the center of the distal end; it is oriented anteromedially-posterolaterally. From the neutral position (Fig. $30A_2$), translation of the astragalar sulci along the tibial condyles of different length resulted in abduction of the hind foot. In this movement, the lateral sulcus translated along the semilunar lateral tibial condyle, whereas the medial sulcus rolled and pivoted about the medial condyle (Fig. $30B_2$). The lateral condyle, furthermore, is spiral; the anterior part of the articular surface faces distally, the posterior part (extending onto the posterior surface of the tibia) posteromedially. This spiral shape caused the astragalus to evert (i.e., the volar surface of the foot turned outward) as it was abducted.

In addition to the excursion at the tibioastragalar joint, the foot had to be plantarflexed in order to secure a grip for headfirst descent (Fig. 30B). This movement occurred at the astragalocalcaneal joint (Figs. $30A_1$, B_1) and involved pivoting the calcaneum about an axis through the sustentaculum tali; the facet of the sustentaculum and its counterpart on the astragalus are nearly equal in size, and thus give no evidence of substantial translatory movement. Excursion at the proximal calcaneoastragalar joint, however, did involve translation. The bulbous proximal calcaneoastragalar facet provided a semilunar pathway, and full plantarflexion involved a degree of conjunct inversion (Fig. $30B_1$).

Additional postural adjustments of the foot for climbing on uneven substrates could have been accommodated at the calcaneocuboid and astragalonavicular joints. The cuboid facet on the calcaneum is slightly concave and is larger than the reciprocally convex facet on the cuboid (Fig. 24). The long axis of the saddle-shaped astragalonavicular joint is oriented dorsolaterally-ventromedially (Fig. 25). Translation of the navicular along this axis would have contributed to inversion-eversion, whereas movements normal to the long axis would have provided additional dorsiflexion-plantarflexion. Conjunct movements at the calcaneocuboid joint appear to have been possible for each of these actions.

The amount of abduction permitted by the tibioastragalar joint was on the order of 90°. Consistent with the degree of femoral abduction reconstructed on the basis of hip structure (see above), the normal stance of the foot probably also involved an abducted posture. Our estimate is that the longitudinal axis of the foot (passing along the third metatarsal) deviated 30° to 40° from a sagittal plane. With an additional 90° of abduction possible at the tibio-astragalar joint, the foot could have readily assumed the posture depicted in Figs. 30 and 31. This posture involved repositioning the tibia and fibula nearly parallel to the vertical substrate, in contrast to the more or less perpendicular orientation in a stance on a horizontal substrate. Such a movement could have been accomplished through hip extension (the femoral condyles of multituberculates indicate that knee extension was limited).

The distal facet on the entocuneiform is saddle-shaped (concave dorsoventrally, convex mediolaterally) and permitted both flexion-extension and abduction-adduction of the hallux. However, the convexity is asymmetrical; the facet extends farther medially than it does laterally, a feature

that is directly indicative of an unusual degree of hallucal abduction.

A divergent, abductable hallux is typical of small mammals that move on uneven surfaces. Mammals that descend vertical surfaces (such as tree trunks) headfirst are capable of reorienting the hind foot, thus pointing the toes backward and positioning the claws to secure a grip. The presence of features in the hind foot of multituberculates that would permit the same kind of behavior may be taken as one line of evidence that some multituberculates, at least, were arboreal in habit.

The characters of the terminal phalanges of both manus and pes indicate well-developed falculae *sensu* Le Gros Clark (1936). Extensive trochleae at the distal interphalangeal joints and protuberant flexor tubercles and extensor processes are evidence of claws capable of strong, gripping action.

Trunk

The partial skeleton of *Ptilodus kummae* (UA 9001) provides an opportunity for reconstructing limb and body proportions (Fig. 31). The fact that the anterior thoracic and the entire cervical series is missing in this specimen requires some extrapolation. The following is an account of how the length of the pre-caudal vertebral column was determined.

The sacral and lumbar regions are completely represented, although some of the vertebrae are crushed or otherwise distorted. The combined length of the four sacral verebrae is ca. 24.5 mm. The lumbar series comprises at least seven vertebrae, and possibly eight. If seven lumbar vertebrae are assumed, the total length of the lumbar series measured along the ventral aspect is 46.5. If the lumbar series is measured from its dorsal aspect, the total length is 44.1. The lumbar series may therefore be safely estimated to be between 40 and 50 mm in length.

Only a few of the posterior thoracic vertebrae are sufficiently well preserved to permit mensuration. Of these, three have centra, 4.0, 4.25, and 4.5 mm in length. On this basis, if it is assumed that the length of thoracic vertebrae decreases anteriorly (as in most mammals) and that the average length of the vertebrae is 4.25 mm, then the total maximum length of the thoracic column is about 51 mm for twelve vertebrae and 55 mm for thirteen. The thoracic series was therefore probably between 45 and 55 mm in length.

In the absence of all cervical vertebrae in this specimen, the length of the neck had to be estimated from the relative proportions known in other mammals. For *Tupaia glis*, *Didelphis marsupialis*, and *Procyon lotor*, the cervical vertebral column ranges from 16 to 22 percent of the total length of the sacral, lumbar, and thoracic series. Using 19 percent as an average, the estimated cervical series length in *P. kummae* would be between ca. 22 and ca. 24.5 mm depending on whether trunk length was as little as ca. 110 or as much as ca. 130 mm.

When these variables are taken into consideration, trunk length estimates range from about 130 to 155 mm for *P. kummae*. In Figure 31 the total length of the precaudal vertebral column is depicted to be 138 mm.

Tail

The tail in mammals may serve a variety of functions: behavioral, protective, thermoregulatory, postural, and locomotor. Among the orders Marsupialia, Rodentia, Edentata, Pholidota, Carnivora, and Primates, some taxa have evolved both

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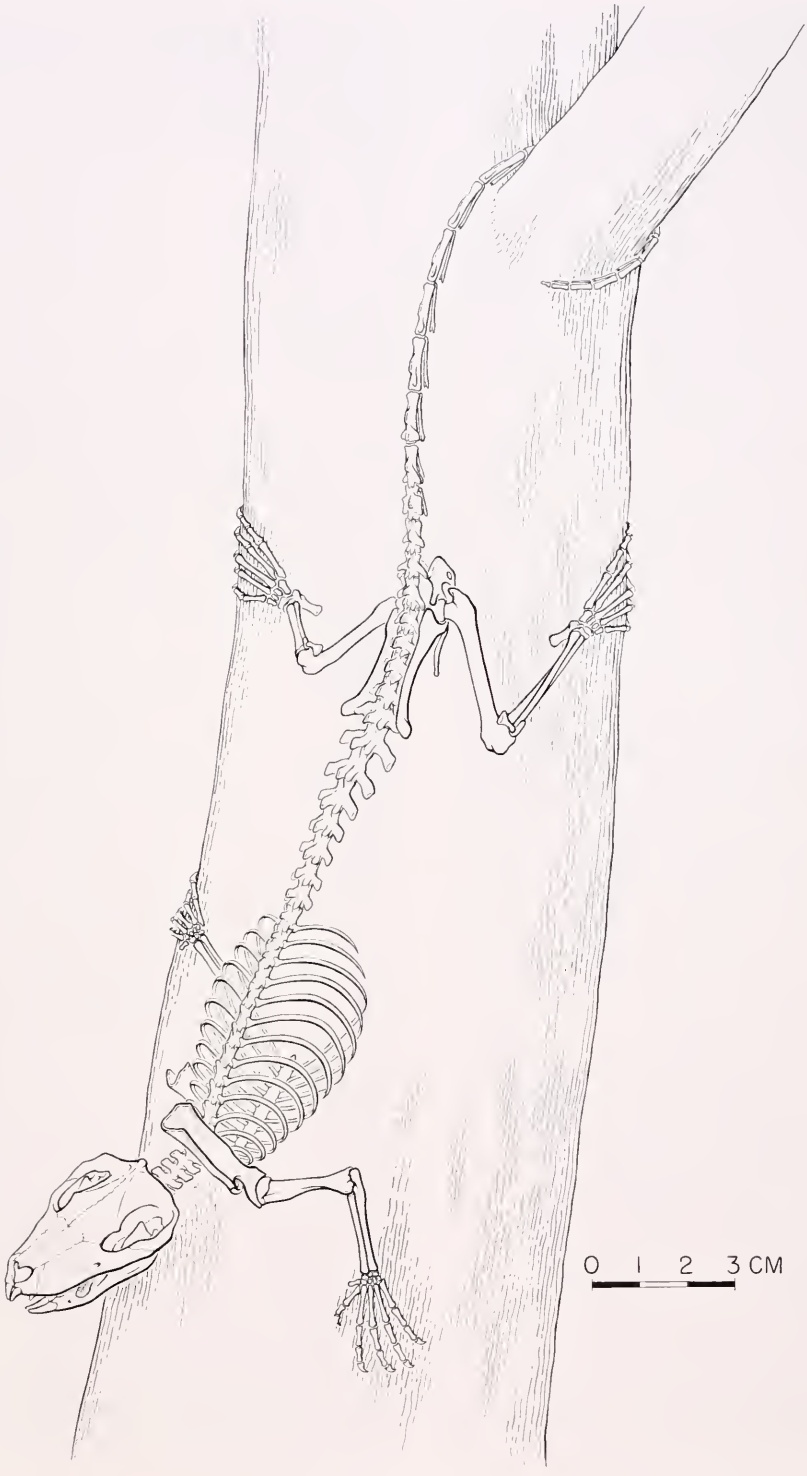
Figure 31. Reconstruction of a multituberculate skeleton based principally on a specimen of *Ptilodus kummae* (UA 9001). The body is positioned in headfirst descent. In this posture the thoracolumbar region is extended, the hind foot is reoriented such that the toes point backward, and the tail is employed as a grasping and stabilizing organ.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musculoskeletal and neural specializations to effect prehensility, that is, the tail is sufficiently robust, and its movements so precisely controlled, as to serve as a "fifth limb." Well-known examples are various species of the genera *Caluromys, Didelphis, Marmosa, Philander, Phalanger, Pseudocheirus,* and *Trichosurus* among marsupials; *Capromys prehensilis, Coendou* spp., and *Pithecheir melanurus* among rodents; *Tamandua tetradactyla* and *Cyclopes didactylus* among edentates; *Manis tricuspis* among pholidotans; *Arctictis binturong* and *Potos flavus* among carnivores; and species of the genera *Cebus, Alouatta, Ateles, Brachyteles,* and *Lagothrix* among primates. All of these taxa employ the prehensile tail in climbing; all may be considered arboreally adapted despite variations in allocation of time spent on the ground or in trees.

A preliminary survey of prehensile-tailed mammals reveals a number of shared features in their caudal structure. The tail is long, commonly twice or more the length of the precaudal vertebral column; in a few taxa the tail is shorter (e.g., in *Didelphis,* where the tail is 1.2 times the length of the precaudal vertebral column). Haemal arches are developed along nearly the entire length of the tail. Transverse processes are robust, and are present even on the most distal caudals. Finally, the sacral spinous processes are relatively large, commonly nearly equalling in height the spinous processes of posterior lumbar vertebrae. The last three features appear to be related to the hypertrophy of the caudal musculoskeletal system necessary for increased gripping strength.

The tail of *Ptilodus kummae* gives evidence of most of these bony features. The tail, estimated at 180 mm, is 1.2 to 1.4 times the length of the precaudal vertebral column. Transverse processes are well developed, even on the distal caudals. Haemal processes are large, and present along the entire length of the tail. The sacral spinous processes, to the extent that their height can be estimated, appear to have been as prominent as those on the posterior lumbar vertebrae. From this evidence, *P. kummae* possessed structural adaptations that, in living mammals, are related to tail prehensility and arboreal habits.

DISCUSSION AND CONCLUSIONS

The present review provides evidence of substantial homogeneity in postcranial structure among North American multituberculates of the suborders Ptilodontoidea and Taeniolabidoidea. Despite the diversity of multituberculates, both in size and in dental specializations, postcranial bones exhibit little variability in proportions or in features distinctive of the order. Our assessment is based on those parts of the skeleton for which there is adequate representation: basal scapulocoracoid, distal humerus, proximal ulna, pelvis, femur, proximal tibia, and calcaneum. Where slight differences are apparent (for example, compare the anterior tip of the ilium in *Ptilodus,* Fig. 8, with that of ?*Eucosmodon*, Fig. 18), they do not appear to be of major functional significance. Confidence in our conclusion that North American multituberculates exhibited little postcranial diversification must be tempered by the realization that most material available at present is disarticulated and dissociated. It is possible that the future recovery of associated skeletons will reveal a modest array of taxon-specific adaptations, especially in proportions. However, in the one comparison (metatarsal III/femur length) permitted by the specimens of *Ptilodus kummae* (UA 9001) and ?*Eucosmodon* sp. (AMNH 16325), there is only a negligible difference (*P.* = .31, *E.* = .29) despite the fact that ?*Eucosmodon* is almost twice as large as *Ptilodus* and is not closely related.

Several workers have speculated on the locomotor habits of multituberculates. Gidley (1909: 621) believed that the "relatively large proportions of the pelvis and

hind limbs strongly suggest that *Ptilodus* was saltatorial . . ." Simpson (1926: 247) alluded to the limb proportions of Recent mammals in reaching his conclusion that *Ptilodus* ". . . was probably a swiftly moving and agile quadruped, and that there is nothing in the known proportions of the limbs which indicate in any certain way a terrestrial or an arboreal habitat." Nonetheless, Simpson (1926: 249) concluded from the herbivorous dentition of multituberculates (and the abundant evidence of trees) that "it would be remarkable if many [multituberculates] were not at least semi-arboreal." In a study of the hind limb of ?*Eucosmodon*, Simpson and Elftman (1928: 15–16) observed that the hind foot had ". . . great flexibility, grasping power with opposable hallux, and . . . sharp claws. Neither in its proportions nor morphological features does this hind foot show fossorial or saltatory adaptations. This and other known characters definitely suggest a quadrupedal animal, well adapted for possible arboreal life but also capable of rapid progression on the ground."

The conclusion from the present study is that some multituberculates, at least, were arboreal in habit (Fig. 31). The primary evidence is derived from the hind foot and tail. In both *Ptilodus* and ?*Eucosmodon* the tibio-astragalar and other tarsal joints are specialized for a range of pedal mobility (especially abduction, permitting headfirst descent) characteristic of arboreal mammals. The hallux was divergent, and the entocuneiform-metatarsal I joint permitted considerable abduction and adduction for prehension in a plane independent of the remaining digits. The long, robust tail of *Ptilodus* possessed musculoskeletal features that, in modern mammals, are present in prehensile-tailed forms. Several other features tend to corroborate this interpretation, although by themselves they are secondary and not definitive evidence: the apparent mobility of the scapulocoracoid and the glenohumeral and hip joints, the large prepollex in *Ptilodus* (possibly augmenting the grasp), and narrow, elongate ungual phalanges with well-developed flexor tubercles and extensor processes (indicating sharp, powerful claws).

Our interpretation of several features in *Ptilodus kummae* as adaptations for climbing does not imply that this or other multituberculate taxa were exclusively arboreal. Jenkins (1974) pointed out that arboreal and terrestrial activity requires basically the same locomotor repertoire of small sized mammals that must climb and grip and span discontinuous substrates in both settings. In the case of tree shrews, for example, species may be either "arboreal" or "terrestial" (or both) in the sense of habitat preference although such a distinction is not evident in musculoskeletal differences. Several tree shrew adaptations (notably the excursions possible in the thoracolumbar region, the shoulder and hip joints, the tarsus and the hallux) are employed in moving and climbing on disordered substrates whether on the forest floor or in trees. Inasmuch as multituberculates appear to have possessed comparable locomotor adaptations, their habitats could have been at least as diverse.

However, two aspects of the postcranial skeleton of *P. kummae*, the structure of the tarsus and tail, represent unusual specializations that in living mammals are used primarily in arboreal locomotion. Furthermore, although evidence for a prehensile tail is available only for *P. kummae*, evidence for tarsal adaptations that permit headfirst descent is known in multituberculate taxa of different body sizes (?*Mesodma* sp., *Ptilodus kummae*, *Stygimys teilhardi*, and ?*Eucosmodon* sp.). *Mesodma*, *Ptilodus*, and *Stygimys* are roughly comparable to tupaiids in size, but *Eucosmodon* is comparable to *Didelphis* and clearly larger than the small mammal size class referred to by Jenkins (1974). Thus, based on present evidence, North American multituberculates over a range of sizes appear to have employed specialized foot postures; because of this, we in-

terpret their specialized tarsal structure as an arboreal adaptation rather than as a response to the locomotor requirements of small mammals.

Multituberculates were a major component of early mammalian faunas, persisting with their characteristic specializations from at least the Late Jurassic to the Oligocene. The possible factors contributing to their extinction have been considered by several workers. Van Valen and Sloan (1966: 277) documented the decrease in multituberculate abundance that took place after a peak in the Late Cretaceous, although they determined that maximal taxonomic diversity occurred during the middle Paleocene. These authors suggested that "the decline of the multituberculates was probably initiated by competition with condylarths, increased by primates, and completed by rodents." Hopson (1967: 354) emphasized that multituberculates were "at best 'submetatherian' in evolutionary grade," but recognized, as did Van Valen and Sloan, that primitive structural features do not necessarily entail competitive disadvantages. Nonetheless, Hopson thought it plausible to suggest an "explanation for the competitive inferiority of the multituberculates to placental herbivores in the early Tertiary: the Cretaceous and earliest Paleocene multituberculates remained significantly below the eutherian level of advancement in nearly all areas of their biology, and their continued survival, and even diversification, depended principally on the fact that they were still the only mammalian occupants of the herbivorous adaptive zone." However attractive is Hopson's hypothesis, our review of the postcranial skeleton of North American forms provides no evidence of features that might be considered significantly inferior to those of eutherians. Skeletal traits that are clearly divergent in multituberculates and eutherians cannot be assessed in terms of comparative locomotor ability, particularly because many such multituberculate features have no analogs among living mammals. The factors contributing to multituberculate extinction, including the possibility of competitive inferiority, must always remain inferential. Yet it is possible to analyze, in terms of function, many skeletal structures in extinct mammals. Such analyses as we have attempted here have been facilitated by other studies, both anatomical and experimental, that have elucidated specific aspects of mammalian postcranial biomechanics. We believe that further advances in our knowledge of multituberculates will depend as much on neontological as on paleontological investigations.

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The Orb-Weaver Genera *Argiope, Gea,* and *Neogea* from the Western Pacific Region (Araneae: Araneidae, Argiopinae)

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THE ORB-WEAVER GENERA *ARGIOPE, GEA,* AND *NEOGEA* FROM THE WESTERN PACIFIC REGION (ARANEAE: ARANEIDAE, ARGIOPINAE)

HERBERT W. LEVI[1]

ABSTRACT. Characters of the male, especially of the male palpus, are useful for studying the phylogeny of the Argiopinae. Members of the subfamily are relatively primitive Araneidae; they appear more advanced than the Nephilinae, Metinae, Tetragnathinae, and Cyrtophorinae, and less advanced than the Mastophorinae, Gasteracanthinae, and Araneinae.

All available types of Pacific and eastern Asian *Argiope* species names have been examined. The study was handicapped by lack of males, which are collected less often than the large, showy females.

The subfamily Argiopinae contains three genera: *Argiope, Gea,* and the new *Neogea. Neogea,* with the type *Araneus egregius,* also contains *Gea nocticolor.* In the region, there are 49 species of *Argiope,* 7 species of *Gea,* and 2 species of *Neogea,* many of them widely distributed. The 12 new species are *Argiope dietrichae, A. katherina, A. kochi, A. mascordi, A. radon* from Australia; *A. boesenbergi* from Japan; *A. ponape* and *A. truk* from the Caroline Islands; *A. caledonia* from New Caledonia; *A. manila* from the Philippines; *A. thai* from Thailand; and *Gea eff* from New Guinea. The generic names *Austrargiope, Coganargiope, Mesargiope, Micrargiope, Chaetargiope,* and *Neargiope* of Kishida and *Brachygea* Caporiacco are subjective synonyms of *Argiope.*

Argiope aequior and *viabilior* are oxyopids; *aurea* and *sachalinensis* are *Araneus; lepida* is probably an *Acusilas; leucopicta* is a *Cyrtophora. Gea virginis* is a *Leucauge.* There are 57 new synonymies.

INTRODUCTION

I undertook this study in order to solve the relationship of the genera *Argiope* and *Gea* to *Araneus* and other orb-weavers. Other reasons for this revision are to make possible the identification and naming of these common, large, showy spiders from the western Pacific area, and to distinguish the related genera *Argiope* and *Gea.*

My studies of American Araneidae began with *Argiope* (1968) because these could easily be sorted from specimens of other genera. Since this was the first genus examined, analysis of the relationships was not possible. Another limiting factor was that there are only two *Argiope* species in Europe, and only seven of *Argiope* and one of *Gea* in the Americas (one additional *Argiope* from Brazil has been found since the publication of my 1968 revision). Only now that I have a fair knowledge of the temperate American and central European araneid fauna am I beginning to discern affinities.

In contrast, the western Pacific region is extremely rich in orb-weavers; 49 species of *Argiope,* 7 of *Gea,* and 2 of a new genus, *Neogea,* are illustrated here. The abundance of species is greatest in New Guinea and Australia. I hoped that by studying a great diversity of species I would develop some insight into which characters are primitive and which specialized.

Because of the increasing amount of literature and the popularity of the large diurnal *Argiope* species for ethological and ecological studies (Robinson and Robin-

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Map 1. The number of argiopine species found in different areas (see text).

son, 1980; Horton, 1981; Olive, 1980), it has become urgent to be able to determine these species, as well as to gain an understanding of their relationship.

This study began modestly as an attempt to help identify the common *Argiope* and *Gea* from New Guinea. Since only a few of the 104 species (87 *Argiope*, 17 *Gea*) and subspecies names of this region listed in Roewer's catalog (1942) [87 species in Bonnet, 1955, 72 *Argiope*, 15 *Gea*] had been illustrated and were recognizable, identification was possible only by examining the types. Most of the species names had never again been cited after the initial description. The scope of the task rapidly ballooned. It was possible only because the females of *Argiope* and *Gea* species are relatively easy to separate, having distinct, sclerotized genitalia. The abdomen, too, is usually marked and shaped distinctively.

Father Chrysanthus (1958, 1971) studied not only the New Guinea *Argiope* and *Gea*, but all species of Araneidae, and worked on various other families also. Apparently overwhelmed by the rich fauna, he unavoidably made mistakes; for instance, he compared his *Argiope* specimens to Indonesian species but not to those from nearby Australia.

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This study was made possible by the help of numerous curators and collectors, in particular, L. Capocaccia and G. Arbocco of the Museo Civico di Storia Naturale, Genova. It is impossible to work with spiders from most parts of the world without access to the Thorell collection, kept mainly in Genova, Italy. Thorell described species and genera, but never made illustrations. Even with illustrations, reference to his collection is essential. I have frequently wondered how Thorell would have fared if forced to rely solely upon his own long-winded Latin descriptions. I now know that he sometimes re-

named his own, previously described species.

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METHODS

In a departure from my procedure with other araneid revisions, I had to look first at the type specimens. I borrowed these a few at a time, illustrated them, and returned them to the various museums before receiving the next batch. Hence, most types could not be compared. Most types

had never been illustrated before, nor had their genitalia been described. Despite the common occurrence and conspicuous appearance of many *Argiope* species, only small collections were available; these usually included only females, rarely escorted by males. The only specimens available throughout the study were collections in the Museum of Comparative Zoology (MCZ). Smaller collections of undetermined *Argiope* specimens were examined at the end of the study.

Since much of the work was done with types of names, I did not illustrate the female internal genitalia. Fortunately, *Gea* and *Argiope* species have other characters that can be used to separate the species.

The size range of individual specimens of both males and females is considerable, although most *Argiope* have similar proportions. No measurements were made. The size and proportions are recorded only for new species; the sizes of previously named species can be read from scale lines on the illustrations. Size range is usually not a good diagnostic character. Although the females of some species are always large, over 20 mm in total length, some species are intermediate in size, and small species may be only 7 to 12 mm in length.

The size range of males (those few that were available) is even broader than that of females. Specimens of any given species (not necessarily collected from the same locality) almost always display wide variability in color and marking. Males of all species were checked for leg modifications such as hook on first coxa, tooth on endite, or tooth on palpal femur. None had any of these modifications, so characteristic of the males of Araneinae.

In matching females with the very different males, it was helpful that most of the males in collections were with females. Those few that had been collected separately could be matched by considering collecting locality and the species group to which they belonged.

Another extraordinary clue expedites matching males with females of the same species. In all species (as far as we know), the tip of the male embolus breaks off and remains in the epigynum (often with a section of the duct pulled out from more proximal sclerites in *A. aemula* and *A. pulchella*). Females can be matched to males by extracting the broken tips (Figs. 250, 261, 262) from the opening of the epigynum. These broken emboli are commonly embedded in hardened exudate within the depression of the epigynum and wedged into the opening (Figs. 82, 124, 136). Just as loss of the embolus tip prevents a male from using the palpus again, having it wedged in the epigynum prevents a female from mating a second time. Although adult females of most species are commonly found with one palpal tip embedded in each side of the epigynum, males with broken palpi are uncommon. Apparently few survive mating. (One male of *A. appensa* from Palau had both palpi broken off above the tibia, as is seen in male eunuchs of *Herennia* from New Guinea [Robinson and Lubin, 1979]). Robinson and Robinson (1980) observed in several *Argiope* species that males died in copula. In the illustrations of epigyna in this monograph, the embolus tips, when present, were removed from one side and not the other (Figs. 82, 124, 136).

The similar *Argiope versicolor* (Doleschall) and *Argiope pulchella* Thorell were considered one species until it was discovered that broken tips in the epigyna differed (Figs. 250, 261, 262).

The emphasis in this paper is on the diagnostic features of the various species. The terms used to point to these differences are illustrated in Figures 12, 13.

With an abundance of species and only a limited number of specimens, decisions had to be made whether minor differences reflect geographic variation or if they represent different species (e.g., *Argiope reinwardti*, *A. caesarea*, and *A. buehleri*, Figs. 42–46, 47–55, 56–60).

Mapping the old collecting localities often proved difficult. There appear to be French, German, and several English

spellings for Chinese place names. Names changed, especially when colonial countries became independent. When the British took over from the Germans in New Guinea after the First World War, names were changed; likewise, the Indonesians changed the Dutch names and spellings.

While taxonomists are reputed to be skeptical, I believe most are too trusting about locality information and data with specimens. Of course, in the case of the well known George Marx spider collection, the specimens quite obviously did not come from the collecting sites indicated. But there are other such instances. Among the collections examined here, I believe that *Argiope carinata* L. Koch bearing a label "New Holland" [Australia] is actually from America, and is a common *A. argentata*. Another, *A. multifasciata* Thorell, allegedly from Singapore, is an Australian *A. protensa*. Such obvious errors raise the question whether other specimens may be wrongly labeled. Some old localities could not be found at all, either because indecipherable handwriting resulted in errors in copying the labels, or because the localities changed names. Some labels give precise locality data but omit the name of the island or continent. Judging by the contents, several vials marked "Plummers Island" did not come from the South Pacific at all, but from an island with this name in the Potomac River, a favorite North American collecting site. Incorrect localities in collections have been reported recently by O. Francke (1981) and von Helverson and Martens (1972).

Lectotypes were designated only when the syntype series received on loan represented several species. Only recent authors have indicated on the label that a particular vial contains types of the name; nineteenth century authors, including Thorell and Simon, did not. Worse, the original specimens may have moved to another institution, perhaps as a result of exchanges (some L. Koch determined specimens of the Godeffroy collection), or been split up, or had other specimens added (as in the Simon collection). Sometimes a syntype series has been incorrectly marked "types" by curators. It is suspected that caretakers sometimes loaned only part of the type series with a new label, failing to indicate that there were additional specimens. While I did not usually choose lectotypes, I did add labels to the vial suspected to be the type, indicating holotype or syntypes.

Roewer (1942) and Chrysanthus (1958, 1961, 1971) spelled the generic name *Argiope* with a *y*. The name *Argiope* (with *i*) has been placed on the Official List of Generic Names in Zoology; *Argyope* (with *y*) has been placed on the Official Index of Rejected and Invalid Names in Zoology (Internat. Comm. Zool. Nomencl., 1975, Opinion 1038). In the literature citations in this paper, to save space, both Chrysanthus and Roewer citations are with *i*.

RELATIONSHIPS

Argiope, *Gea*, and the new genus *Neogea* are the only genera in the subfamily Argiopinae of the family Araneidae. The subfamily is characterized by having the posterior eye row procurved; that is, the posterior lateral eyes anterior to the posterior medians (Figs. 27, 39, 52). In other Araneidae posterior lateral eyes are at the same level or slightly posterior to the posterior medians. *Gea* and *Neogea* differ from *Argiope* in having the posterior eyes equally spaced (Figs. 348, 353, 402). *Argiope* has the posterior median eyes farther from laterals than from each other.

The following are characters for the cladogram.

1. *Orientation of the Sclerites.* The sclerites of the palpus face the median, with the cymbium pushed to the side of the sclerites, left in the left palpus (Figs. 7, 8, 13) (or, the cymbium moved in a median direction, the tegulum dorsal, and the sclerites ventral). This is a synapomorphy shared by the Argiopinae, Mastophorinae, and Araneinae. In all other spiders the sclerites face ventrally with the

cymbium dorsal. (Originally I considered *A. trifasciata* intermediate in this respect, as the embolus coil faces ventrally [Fig. 119], but after examining numerous *Argiope* and *Gea* species, I find that this orientation arises from the extension of a specialized palpus with a long embolus. The long, coiled embolus has secondarily moved ventrally.) This character indicates that I can use Nephilinae, Tetragnathinae, and Metinae as outgroups for the remaining characters.

2. *Eye Position.* The procurved posterior eye row is only found in *Argiope*, *Gea*, and the new genus *Neogea*, and is a synapomorphy of these genera not otherwise found in the family (except rarely in some species of the genus *Mecynogea*). Outgroup comparison with the Tetragnathinae, Metinae, Nephilinae, and comparison with the subfamilies sharing the same orientation of the male palpal sclerites indicate the derived nature of the eye arrangement. The Argiopinae eye arrangement is accompanied by a characteristic marked reduction in the size of the anterior lateral eyes: they face down, and their diameter often is only half that of the other eyes (which are subequal in size), so small that in dorsal view they are not visible (Figs. 3, 5).

3. *Posterior Median Eye Structure.* Members of the superfamily Araneoidea have a canoe-shaped tapetum (found also in Agelenidae, Clubionidae, Anyphaenidae, and Gnaphosidae, among others). Some araneid orb-weavers have a canoe-shaped tapetum, others have the eyes more specialized. The canoe-shaped tapetum is still found in *Meta* and relatives, *Zygiella*, *Leucauge*, *Nephila* (Levi, 1980: figs. 37, 38). In the subfamily Tetragnathinae, there is a loss of the tapetum in the posterior median eyes of *Pachygnatha* (Levi, 1980: fig. 159), and in all eyes of *Tetragnatha* (Levi, 1981). In *Araneus* and most Araneidae other than Tetragnathinae, Metinae, and Nephilinae, the tapetum of the posterior median eyes shrinks to a sliver, and the rhabdom cells toward the median (of the spider) arrange themselves in rows (Fig. 10; Levi, 1978: figs. 19, 20), while the lateral eyes keep the canoe-shaped tapetum. It is a synapomorphy shared by Cyrtophorinae, Argiopinae, Mastophorinae, and various genera (most of which belong to the Araneinae).

4. *Posterior Lateral Eye Structure.* In *Argiope*, *Gea*, and *Neogea* the tapetum shrinks in the posterior lateral eyes as well as in the posterior medians (Figs. 9–11). This probably provides better daytime vision. I consider this unusual specialization of the posterior lateral eyes not otherwise found in the family Araneidae or the Araneoidea (first pointed out by Homann, 1950) to be a synapomorphy of these three genera.

5. *Carapace Shape.* The head of female is more distinctly set off from the thoracic region than in other Araneidae. In *Argiope* the head width is half that of the carapace; the sides of the head are parallel, the front edge almost straight in dorsal view, and the lateral eyes on slight tubercles (Figs. 22, 39, 45). The small anterior lateral eyes face down and are hidden in dorsal view (Figs. 3, 5); the carapace is almost circular and relatively flat, often with two comma-shaped marks in the thoracic depression. In *Gea*, which has relatively larger eyes, the head is wider and less distinctly set off (Figs. 341, 348, 353); the anterior lateral eyes are also small (Figs. 334, 336). Other genera with a narrow head are *Acusilas* of southeastern Asia and *Cyclosa* and *Mangora* (all probably Araneinae). In all of these the sides are not so parallel, and the head region is more domed. I consider the head shape and small anterior lateral eyes a synapomorphy in *Argiope*, *Neogea*, and some species of *Gea*. It has probably secondarily been lost and become more generalized in *Gea*. I assume that the distinctive procurved posterior eye row is correlated with the shape of the head.

6. *Abdomen Shape and Color.* The abdomen is usually shield-shaped, often lobed on its sides, flattened, and brightly

patterned in *Argiope*, *Gea* and *Neogea* (Figs. 27, 45, 70, 78). Silver and black are common colors. Similar abdomen shape is found in the unrelated *Herennia*. (Judging by the structure of the genitalia, especially the male palpus, *Herennia* is closely related to *Nephila*, Nephilinae.) Bright coloration is found in the predominantly diurnal American species of *Alpaida*. In some Australian *Argiope* species, the abdomen has a semblance of a dorsal folium, the dark leaf-shaped pattern (Figs. 122, 139, 191) commonly displayed by the Araneinae.

A cylindrical abdomen is found in *Nephila* (Nephilinae), *Leucauge* (Metinae), *Tetragnatha* (Tetragnathinae), *Cyrtophora* and *Mecynogea* (Cyrtophorinae); a spherical abdomen in most other Araneidae. Perhaps a cylindrical body (of *Argiope ocula* and *A. thai* is a primitive character of the family. However, color and abdomen shape probably are characters of ambiguous polarity in pinpointing phylogeny, and I use the spherical abdomen (a weak character) as a synapomorphy of Mastophorinae, and the remaining genera, most of which belong to the Araneinae.

7. *Leg Length.* *Argiope* and *Gea* have longer legs than most Araneidae. Other long-legged araneids are *Tetragnatha* species. In *Argiope* and *Gea*, legs one and two are subequal in length, the second slightly shorter than the first, the fourth leg usually slightly shorter than the second, the third by far the shortest. The first legs may be 1.3 to 1.8 carapace length; the second 1.2 to 1.6; the third, 0.6; the fourth 1.2 to 1.4. At present I am not certain of the distribution of leg length in araneid genera, and find the leg proportions confusing to use for phylogeny; they may be adapted to selection pressures of the spider's habits (Olive, 1980) which have been recurrent during phylogeny. Perhaps after studying the species of more tropical genera a phylogenetic use of leg length will emerge. I do not use this character at present.

8. *Male Size.* The small size of males is most striking compared with the large size of females in *Argiope*. Within a species, the males vary substantially in both size and coloration, making them difficult to match to females of the same species. Small males are found also in *Nephila* and other predominantly tropical genera (which have year-round reproduction, permitting the more rapidly maturing males to mate with a previous generation of females). Vollrath (1980) has recently commented on the small sizes of males. I will know more about the distribution of this character after a study of various tropical Araneidae. At present I do not use this character in phylogeny.

9. *Male First and Second Legs.* In males of most Araneinae the first or second legs are modified with extra macrosetae, bumps, and branches (e.g., *Acacesia*, *Aculepeira*, *Eriophora*, *Verrucosa*), probably to hold the females when mating. Such modifications are lacking in *Argiope*. As males of some *Gea* species have stronger setae on their legs than their females have, and in *Gea* the sexes are more nearly equal in size than in *Argiope*, I assume that in *Gea* the strong leg spines are a modification for coping with similar sized females. Leg modifications are lacking also in Nephilinae, Metinae, and Tetragnathinae, in some of which (Tetragnathinae) the sexes lock chelicerae when mating. These leg modifications are of little use for phylogeny of possible subfamilies, probably reflecting more equal size of the sexes. I do not use this character here, but may return to it in future papers.

10. *Other Modifications.* In many species of Araneidae males have a tooth on the outside of the endite, facing a tooth on the palpal femur. They also have a distal hook on the first coxa that fits into a slit on the second femur, presumably locking the two legs in mating position. Neither structure is ever found in Nephilinae, Tetragnathinae, Metinae, Cyrtophorinae, Argiopinae, or Mastophorinae. These fea-

tures are usually present but sometimes absent in the Araneinae, perhaps secondarily lost (in *Araneus gemmoides* and also some small-sized species). I take these characters to be synapomorphous among the genera belonging to the Araneinae, although they may have been lost secondarily in some species. (Male *Micrathena* may have the coxal hook; many species lack it. They never have a tooth on the endite or a tooth on the proximal end of the palpal femur, probably secondarily lost.)

11. *Epigynum.* The epigynum lacks a scape in most *Argiope* and all *Gea* and *Neogea*. A scape is present in most Araneidae, although not in Nephilinae, Metinae (except some *Zygiella*), and Tetragnathinae. The scape is also absent in those Araneidae species having a heavily sclerotized epigynum (e.g., *Gasteracantha*, *Micrathena*). But the presence of a scape in some species of *Zygiella* (a genus whose members have a canoe-shaped tapetum in the eye and a tegulum apophysis in the male palpus; Levi, 1974) and in some *Mysmena* (Mysmenidae) species, as well as in some species of *Pityohyphantes*, *Helophora*, *Lepthyphantes* (Linyphiidae), and in *Wendilgarda* (Theridiosomatidae) is convincing evidence that the scape evolved several times as a convenient coupling device. The presence or absence of the scape, therefore, is not a useful character in phylogeny. It is of interest that *Argiope ocula* has a well-developed scape (Fig. 14). This species has also several other characters that I consider primitive: the posterior eye row is only slightly procurved, and the abdomen is cylindrical. *Argiope macrochoera*, which has an indication of a scape (Fig. 19), is perhaps not closely related to *A. ocula*, judging by abdomen shape and general epigynal structure.

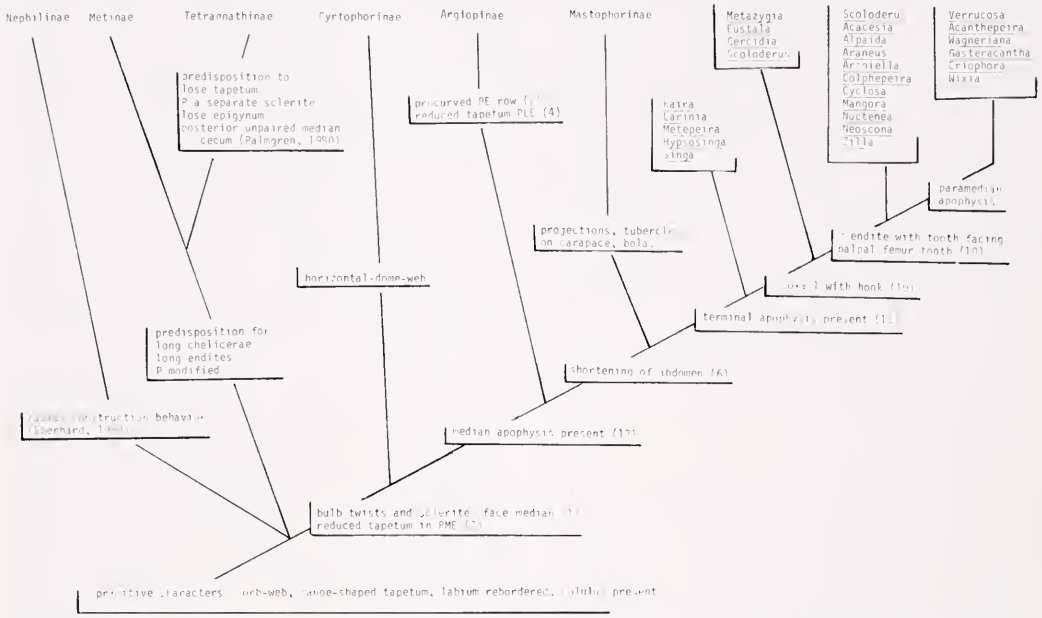
12. *Terminal Apophysis.* The Argiopinae lack a terminal apophysis in the male palpus. There is also no terminal apophysis in Nephilinae, Metinae, Tetragnathinae, Cyrtophorinae, and Mastophorinae. There is a terminal apophysis in Araneinae and related genera, a synapomorphy of the genera included. The terminal apophysis in some linyphiids and mimetids may not be homologous with that of Araneinae.

13. *Median apophysis.* The median apophysis is absent or very small in the male palpus in Nephilinae, Metinae, Tetragnathinae, and Cyrtophorinae. It is always present as a large structure on Argiopinae (Fig. 13), Mastophorinae and the various genera, most of which are placed in the Araneinae. I consider this a synapomorphy of the genera within these groups. (The lobe present in some species of Cyrtophorinae in place of the median apophysis may not be homologous with the median apophysis.)

14. *Spur of the Median Apophysis.* The spur of the median apophysis is almost always thread-shaped in *Argiope*, *Gea*, and *Neogea* (Fig. 13). Exceptions are the thorn-shaped spur in *A. ocula*, perhaps a primitive feature, and the loss of the spur in *A. trifasciata*. The spur of the median apophysis of other genera is almost never filamentous (an unusual exception is that of *Micrathena gracilis* species group). I consider the thread-shaped nature of the spur of the median apophysis a synapomorphy of the genera in Argiopinae.

15. *Embolus and Conductor.* Unlike that of other araneid genera, the embolus and conductor of the male palpus is often enlarged, frequently extending far beyond the spherical tegulum (Fig. 13). The embolus and conductor of *Nephila*, *Pachygnatha*, and *Tetragnatha* is also large. But since the bulb has not twisted (see above, no. 1), the configuration differs, and the large embolus and conductor is probably a convergence. There are *Argiope* species in which these structures are relatively small, probably a primitive condition: *A. aemula* and *A. catenulata*. The kink and pendant displayed by members of the *A. aetherea* group (Fig. 13) is a specialization, as is the coil of *A. trifasciata*. Phylogenetically, the straight em-

TABLE 1. CLADOGRAM OF SUBFAMILIES OF THE ARANEIDAE.



Abbreviations. P, paracymbium; PE, posterior eyes; PLE, posterior lateral eyes; PME, posterior median eyes. Numbers in parentheses refer to paragraphs in the text.

bolus and conductor of *A. aurantia* would place this species near the center of the *Argiope* species. The large size of embolus and conductor is an uncertain synapomorphy of the Argiopinae.

Comment. When making the simple computer cladogram (Levi, 1980: table 2) I was concerned that only slight changes in weighting of characters would result in major changes in the cladogram. Here the groups are nested according to their most unusual specializations (Table 1).

My ideas on phylogeny and relationships are changing as I study these genera a second time. For instance, *Cyrtophora* and *Mecynogea*, previously placed in the Araneinae (Levi, 1980), are here relegated to their own subfamily (Table 1). An expansion of thoughts on possible araneid-uloborid relationships is found in Coddington (in preparation) and Eberhard (1982). The Theridiidae, Nesticidae, and Linyphiidae probably had Metinae-like ancestors and branched off from the base of the branch of the Metinae and Tetragnathinae (Table 1). Shear (1981) also would place the origin of the Mimetidae in this vicinity. This would make the family Araneidae as here presented paraphyletic. But is this really objectionable in a classification?

DISCUSSION

Despite 11 new species of *Argiope* and 1 new *Gea*, the total number of species for the area is only slightly more than half the number listed (to 1938) in Roewer's catalog of spiders. The other names listed are actually synonyms, the result of inadequate descriptions. (When the synonymies revealed here could be attributed to obvious similarities in genitalia and abdomen coloration and structure, no further reason for the synonymy is given.)

Many species have enormous ranges: *A. bruennichi* from western Europe to Japan; *A. lobata* from the Mediterranean to

Java and perhaps New Caledonia, Australia, and Africa; and *A. trifasciata*, common in the Americas, Hawaii, Australia, and North Africa. Many other species are probably restricted in distribution, although this is difficult to ascertain because of inadequate available collections.

The greatest number of species of the group is found in New Guinea and Australia. The number declines towards the Asian mainland: There are 6 in Japan and Korea, 8 in China and Taiwan, 9 in India, 9 in southeastern Asia (Malayan Peninsula, Burma, Thailand), 12 in Java and Sumatra, 6 in Borneo, 7 in the Philippines, 18 in New Guinea, and 11 in Queensland, Australia (see Map 1).

Unlike most spiders, *Argiope* are large and showy, usually hanging in conspicuous webs in the open (Plate 1). Most species were named during the 19th or early 20th century. *Argiope* also has been fairly well collected. Of the 11 new species in the subfamily 6 come from Australia; 2 from the Caroline Islands; and 1 new species each from New Guinea, New Caledonia, Solomon Islands, Philippines, and Thailand. Since most museum collections available are the result of efforts by amateurs, the collections contain a preponderance of females and only very few of the small males.

Most species are very distinct and can be separated by genitalia as well as by their appearance. There are several exceptions: *Argiope versicolor* and *A. pulchella* in southwestern Asia to Indonesia are similar in appearance and also have quite similar genitalia. Also *A. taprobanica* and *A. versicolor* have a similar pattern. Their distributions overlap. Another such group (but with allopatric distribution) is *A. reinwardti* from Indonesia to New Guinea and *A. caesarea* from Burma and India; perhaps this is just a geographic variant of *A. reinwardti*.

Argiope species apparently have inherited a developmental capacity for various coloration, and similar patterns reappear in several unrelated species (Figs. 22, 45, 170, 208, 244, and 257).

Another problem is the *Argiope aetherea* group. *Argiope aetherea*, described from New Guinea, is quite variable in appearance, its abdomen ranging from banded to having only a black posterior tip (Figs. 303, 305). The sympatric *A. picta* (originally described from Australia) has a different abdominal shape and pattern. Yet the genitalia, especially the epigyna, are disconcertingly similar. Are the specimens here labeled *A. aetherea* from Australia really the same species? (In most, the sternum is not such a bright yellow as in New Guinea specimens, but Australian specimens also come with banded or black tipped abdomen.) *Argiope brunnescentia*, from the Bismarck Archipelago and eastern New Guinea, is probably distinct; its range overlaps with that of *A. aetherea*. But are *A. aetherea*-like specimens from the Solomon Islands and New Hebrides (Figs. 306, 307) and *Argiope truk* (from Truk Island, Caroline Islands) separate or just subspecies of the variable *A. aetherea*?

While a published monograph may appear to provide definite solutions, and readers infer that the author is certain of his findings, more likely the work only identifies and illuminates tantalizing problems. Especially to those with no experience with taxonomic problems, a published monograph has an unfortunate aura of authority.

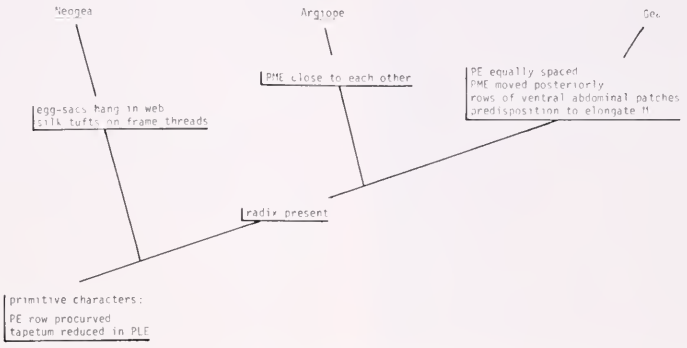
Subfamily Argiopinae Simon, 1890

Argiopidae Simon, 1890: 81. Type genus *Argiope*.
Argiopinae Simon, 1895, Histoire Naturelle des Araignées, 1: 759.

Diagnosis. Argiopinae differ from Araneinae and other subfamilies of the Araneidae by having the posterior eye row procurved when seen from above (Figs. 27, 52, 348, 402).

The posterior eyes differ structurally from those of other subfamilies of the Araneidae: both the laterals and the medians have the canoe-shaped tapetum reduced to a sliver; rows of rhabdoms lacking tapetum are arranged along the side (to-

TABLE 2. CLADOGRAM OF THE GENERA OF THE SUBFAMILY ARGIOPINAE.



Abbreviations. M, median apophysis; PE, posterior eyes; PLE, posterior lateral eyes; PME, posterior median eyes.

ward the median of the animal) (Figs. 9–11). The anterior lateral eyes are much smaller than the others and have a full canoe-shaped tapetum (Figs. 9, 11).

Structure and Color. The head is small in Argiopinae compared to the wide, almost circular thorax. The lateral eyes are on a tubercle; the small anterior laterals cannot be seen from above, as they face forward and slightly to the side (Figs. 1–6). The chelicerae are weaker than those of *Araneus*, with a smaller boss at the base. There are usually two comma-shaped depressions in the carapace. The carapace is almost always covered with white or silver down. The legs are relatively longer than in genera of the Araneinae. The first and second legs are subequal in length; the fourth is slightly shorter, the third much shorter. The abdomen is never spherical, rarely cylindrical (Fig. 16), often ovoid (Fig. 33), pentagonal (Fig. 45), sometimes lobed along the sides (Fig. 93), and often dorso-ventrally flattened. The abdomen is often brightly colored with silver or gold and black on the dorsum, and usually with two white paraxial lines on the venter (Figs. 23, 28, 79, 333). Some species can instantaneously change the color of the abdomen when dropping out of the web (Sabath, 1970; Bristowe, 1976).

The epigynum usually lacks a scape, but almost always has a septum (Fig. 12). Sometimes the openings face dorsally and are hidden below a projection from the genital area (Figs. 81, 82, 99, 100). The epigynum usually has an anterior bulge, a more or less transverse rim, and a pair of depressions separated by a septum which is usually continuous anteriorly with the rim. Posteriorly the septum widens into a posterior plate (Fig. 12). The openings are within the depression, sometimes a slit with lips or a round opening (Fig. 12).

The males are much smaller than females, and never have modified legs, except that stronger macrosetae are found occasionally in *Gea* species. Males have no hook on the first coxae, and lack a tooth on the outside of the endite and on the base of the palpal femur.

The male palpus is complex and always has a small median apophysis (larger in *Gea* species), a large embolus, sclerites between the tegulum and embolus (the stipes) in *Gea* and *Argiope*, and a large conductor. There is never a terminal apophysis (Fig. 13).

Natural History. All *Argiope* and *Gea* are diurnal spiders that rest in the center of the web, head down. Many species have a stabilimentum in the web (Plate 1). The stabilimentum may have only two lines (*A. aurantia* in America); more commonly it has four lines which may not all be present (Robinson and Robinson, 1980).

Possibly the stabilimentum functions to warn potential predators that bill and feathers are likely to be gummed up by silk threads (Horton, 1981). Olive (1980) tried to describe the niches of *Argiope* species as compared with *Araneus* species.

Genera. The subfamily has three genera: *Argiope*, *Gea*, and the new genus *Neogea*. The larger posterior median eyes of *Gea* have evolved at least twice, once in *Gea* and a second time in some of those species here placed in the new genus *Neogea*.

The genus *Argiope* has at various times been split into numerous smaller genera (Kishida, 1936). I do not find this fragmentation into monophyletic genera useful; the numerous names are confusing.

KEY TO GENERA

1. Female abdomen black, with discrete white spots on dorsum as in Figs. 395, 402, 404; epigynum not sclerotized (Figs. 393, 399, 401); male without stipes in palpus (Figs. 397, 406) ..... *Neogea*
– Female abdomen otherwise (Figs. 27, 39, 373); male always with a stipes in palpus (Figs. 13, 387) 2
2. Posterior median eyes closer to each other than to laterals in adults (Figs. 27, 45, 64) ..... *Argiope*
– Posterior median eyes equally spaced (Figs. 348, 353, 371) ..... *Gea*

Argiope Audouin

Argiope Audouin, 1826: 121. Type species designated by Thorell, 1869: 51: *Argiope lobata*. Opinion 1038 of Int. Comm. Zool. Nomencl. (1975) validates the generic name and places the name on the Official List of Generic Names in Zoology with the name no. 2009. Various other spellings of the name have been invalidated.

Miranda C. L. Koch, 1835: 128, pl. 14. Type species *Miranda transalpina* C. L. Koch [=*Argiope bruennichi* (Scopoli)].

Metargiope F. P.—Cambridge, 1903: 451. Type species by monotypy *A. trifasciata*.

Austrargiope Kishida, 1931: 129*. Type species by original designation and monotypy *Austrargiope plana* (L. Koch) [=*A. trifasciata*]. NEW SYNONYMY.

Coganargiope Kishida, 1931: 129*. Type species by original designation and monotypy *Coganargiope amoena* (L. Koch). NEW SYNONYMY.

Mesargiope Kishida, 1931: 130*. Subgenus of *Coganargiope*. Type species by original designation and monotypy *Coganargiope* (*Mesargiope*) *aetherea* (Walckenaer) [misidentification of *A. boesenbergi* n. sp.]. NEW SYNONYMY.

Micrargiope Kishida, 1931: 130*. Subgenus of *Coganargiope*. Type species by original designation and monotypy *Coganargiope* (*Micrargiope*) *minuta* (Karsch). NEW SYNONYMY.

Chaetargiope Kishida, 1931: 130*. Type species by original designation and monotypy *Chaetargiope* (*Chaetargiope*) *picta* (L. Koch). NEW SYNONYMY.

Neargiope Kishida, 1931: 131*. Subgenus of *Chaetargiope*. Type species by original designation and monotypy *Chaetargiope* (*Neargiope*) *regalis* (L. Koch) [=*A. aetherea*]. NEW SYNONYMY.

Brachygea di Caporiacco, 1947: 24. Type species by original designation and monotypy *B. platycephala* di Caporiacco [=*Argiope trifasciata* (Forskål)]. NEW SYNONYMY.

Diagnosis. Argiope is separated from *Gea* and *Neogea* by the arrangement of eyes in females, and usually in males: the posterior median eyes are closer to each other than to the laterals in *Argiope* (Figs. 27, 45, 64). Also, the head region bearing the posterior median eyes is lower than in *Gea* and *Neogea*, and the carapace is relatively wider in the thoracic region (Figs. 1, 3, 5).

Coloration. The carapace is usually covered with white or silver down. Although females of *Argiope* species have a number of unusual patterns on the abdomen, similar patterns appear in groups unrelated to one another, judging relationship by genitalic structure (e.g., *A. trifasciata* markings are displayed also by *aemula* and *magnifica*; *reinwardti* markings by *aetherea*, *luzona*, *amoena*, and *keyserlingi*). Species with very similar genitalia often have very different color markings, which facilitate their diagnosis; thus, *Argiope aetherea* and *A. picta* of New Guinea are more easily separated by pattern than by genitalic structure (Figs. 297–307, 310–314). The venter of the abdomen is usually black with two paraxial

* Original not available; all from Kishida, 1936: 14–27.

white lines enclosing paired white spots. This ventral pattern may be diagnostic (e.g., *A. catenulata*, Fig. 40; *A. bougainvilla*, Fig. 290).

Structure. Argiope species have a narrow head, contrasting with a very wide thoracic region (Figs. 1–7); the chelicerae are relatively weak. Some specimens have a tubercle on the sternum opposite each coxa. The legs are long, the first longest, the second almost as long, the fourth shorter, the third very much shorter. The shape of the abdomen varies from cylindrical (Fig. 16) to oval (Fig. 289), pentagonal (Fig. 27), or shield-shaped (Fig. 313).

Behavior. Argiope make a characteristic orb-web, usually with a stabilimentum (Plate 1). Much of what is known of both web and mating behavior is reported in M. H. Robinson and B. Robinson (1980).

Species. There are 49 species in the Pacific area, including eastern Asia, 2 species in Europe, 7 in the Americas, and about 10 in Africa and western Asia.

Distribution. Argiope species are found worldwide, absent only from the coldest regions.

Species groups. There are several distinct species groups and numerous species not close to others. Characters for males, especially their palpi, are useful not only to separate the subfamilies of Araneidae, but also for understanding relationships at the species level. Unfortunately, for many species the males are not known.

1. *Argiope ocula* group: *Argiope ocula* has a characteristic triangular scape (Fig. 14), an unusual plesiomorph feature; the posterior eye row is only slightly procurved, and the abdomen is cylindrical, another primitive feature. However, as in more specialized *Argiope*, the conductor and embolus extend beyond the tegulum (Fig. 18). The presence of a scape in the epigynum of *A. macrochoera* (Fig. 19) and *A. manila* (Fig. 24) may relate them to *A. ocula*, but more likely it is a convergent structure.

2. *Argiope aemula* group: Females are characterized by the swollen rims and lateral margins of the epigynum (Figs. 29–32, 36–38). The small, short embolus of *A. aemula* and *A. catenulata* are primitive (Figs. 35, 41). To this group belong *A. aemula* and *A. catenulata.*

Plate 1. *Argiope versicolor* (Doleschall). Female from Sarawak with web having an unusually dense stabilimentum (photo to F. Wanless).

3. *Argiope reinwardti* group: Members of this group have a wide median septum in the epigynum (Figs. 42, 47, 56). The only male known, that of *A. reinwardti*, has a relatively short embolus and conductor (Fig. 54). The group includes *A. reinwardti*, *A. buehleri* and *A. caesarea.* Since they are allopatric, they may all belong to the same species.

4. *Argiope amoena* group: Females have the epigynum modified anteriorly (Figs. 61, 67, 73). In males, the embolus is long and straight, held by a straight projecting conductor (Figs. 66, 72, 80). To this group belong *A. boesenbergi*, *A. amoena*, and *A. magnifica. Argiope bruennichi*'s palpus is close to this group, but the much modified epigynum has lost the septum and is pulled posteriorly (Figs. 81–83). Also, the American *A. aurantia* may belong to this group.

5. *Argiope trifasciata* group: Females of many species have a tail on the abdomen (Figs. 104, 110). The epigynum may be lightly sclerotized. In males of many

species the embolus and conductor are longer and more elaborate than in the *amoena* group (Figs. 106, 111, 119). To this seemingly specialized group belong species having a folium pattern on the abdomen (Figs. 122, 139), perhaps a primitive feature seen commonly in females of other subfamilies. *Argiope trifasciata*, *A. protensa*, *A. probata*, *A. bullocki*, *A. ocyaloides*, *A. dietrichae*, *A. doboensis*, and *A. chloreis* belong here; perhaps also *A. katherina*. The American species, *A. argentata*, *A. florida*, *A. blanda*, and *A. savignyi* also belong here.

6. The *Argiope anasuja* group includes mostly small species which tend to have a flange on the rim of the epigynum (Figs. 12, 167). The males of only a few species are known. Included in this group are *A. minuta*, *A. perforata*, *A. halmaherensis*, *A. possoica*, *A. mascordi*, *A. keyserlingi*, *A. kochi*, and *A. caledonia*.

7. *Argiope aetherea* group is the largest, the most distinct, and perhaps the most specialized. The species are often, judging by their genitalia, closely related and fairly specialized. Females of the group are characterized by a relatively narrow epigynal rim, a septum, and in most species a tubercle on the margin on each side of the posterior plate in posterior view (Fig. 12). In males the embolus is curved and describes a semicircle; in many species there is a kink between semicircle and tip (Fig. 13). Other members of the group are: *A. luzona*, *intricata*, *modesta*, *pulchella*, *versicolor*, *appensa*, *brunnescentia*, *bougainvilla*, *pentagona*, *picta*, *radon*, *ponape*, *taprobanica*, and *truk*.

Species of doubtful placement include *Argiope thai*, *takum*, and *niasensis*, in all of which the male is not known. *Argiope lobata*, with males known, is not close to any group.

M. H. Robinson and B. Robinson (1980) divide courtship and mating behavior of tropical araneid orb-weavers into three groups, with that of some *Argiope* in Group A, that of others in Group B, and that of a *Gea* in Group C. They consider Group A behavior to be primitive, Group B intermediate, and Group C the most advanced. They also believe that the behavior of Group C may have evolved several times. My findings here agree in general with this assessment. *A. reinwardti* of Group A is certainly one of the most primitive *Argiope*. *Argiope magnifica* [*A. aemula*: Robinson and Robinson] and *A. aurantia* have specialized features, although of Group A. Group B includes *A. picta*, *A. aetherea*, and *A. radon*, the most specialized *Argiope*. But the group also includes *A. aemula* ("Wau No. 5" and "Singapore No. 1"), which I would consider a species with primitive morphological features. *Gea eff* ("Wau No. 1"), placed in Group C with other species of *Gea*, I consider more specialized than any *Argiope* (Table 2).

Misplaced *Argiope*

Argiope aequior Chamberlin, 1924: 16, pl. 4, fig. 33, ♂. Male from N. Gist Gee, Soochow, China in the U.S. National Museum of Natural History, Washington, examined, is an oxyopid.

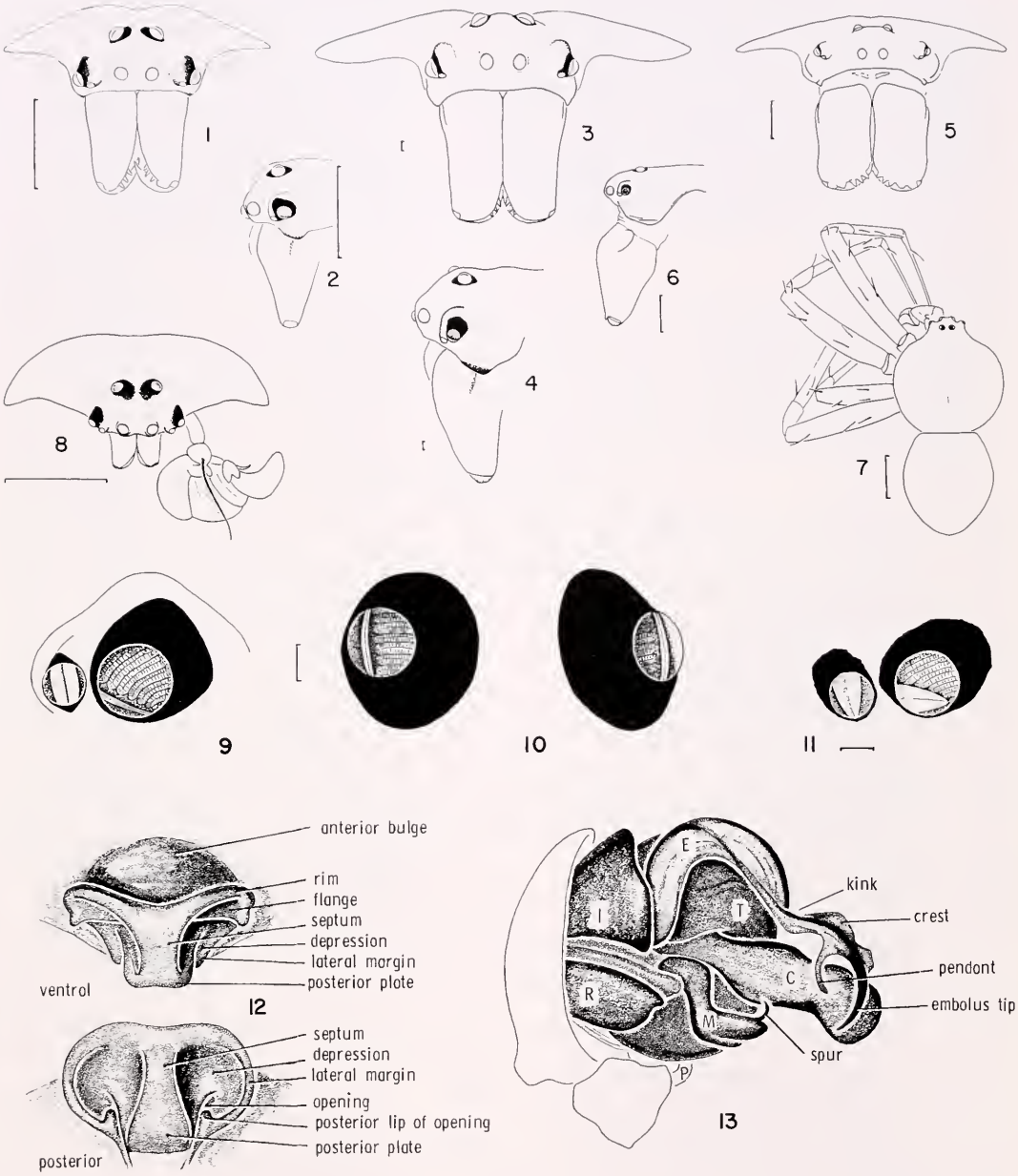
Argiope aurea Saito, 1934a: 316, pl. 13, fig. 20, pl. 15, fig. 63, ♀. The illustrations show a wide head, recurved posterior eye row, and the epigynum having the remains of a scape which has been torn off. It is a relative of *Araneus*.

Argiope carinata L. Koch, 1871: 29, pl. 2, fig. 7. Juvenile holotype and fragments of paratype in poor physical condition, broken, bleached and shrunken, from "New Holland" [Australia] in the Naturhistorisches Museum, Wien, examined. The shapes of the abdomen and ventral markings are distinct, like those of *A. argentata*. No species similar to *A. argentata* is known from Australia. There is a mistake in the locality label; it comes from America.

Argiope lepida Thorell, 1898: 337. Male holotype from Mount Carin [Karen] Chebà, Burma in the Museo Civico di Storia Naturale, Genova, examined, is probably the male of *Acusilas coccineus* Simon, 1895. It has a very narrow head and a strongly recurved eye row.

Argiope leucopicta Urquart, 1890: 234. Female holotype from Fiji Islands, lost. It is not in the Otago Museum, Dunedin, nor in the Canterbury Museum, Christchurch. The description of the recurved posterior row of eyes and color pattern of the abdomen suggest that this is a species of *Cyrtophora*.

Argiope maja Bösenberg and Strand, 1906: 201, fig.



Figures 1–13. *Argiope morphology.* 1–6. Female eye region and chelicerae, face view and lateral. 1, 2. *A. doboensis.* 3, 4. *A. versicolor.* 5, 6. *A. aetherea.* 7, 8. Male, dorsal view and eye region and chelicerae, *A. picta.* 9–11. Female secondary eyes. 9, 11. Left lateral eyes. 10. Posterior median eyes. 9, 10. *A. aemula.* 11. *A. trifasciata.* 12. Diagrammatic epigynum. 13. Left male palpus, mesal.

Scale lines. 1.0 mm, except Figures 9–11, 0.1 mm.

Abbreviations. C, conductor; E, embolus; I, stipes; M, median apophysis; P, paracymbium; R, radix; T, tegulum.

1, ♀. Female holotype from Yokohama, Japan, lost. This is probably *Nephila clavata* L. Koch.

Argiope sachalinensis Saito, 1934b: 332, fig. 6, ♀. The epigynum in Saito's illustration of this species from Sachalin [Sakhalin] has an annulate scape. The species is probably an *Araneus*.

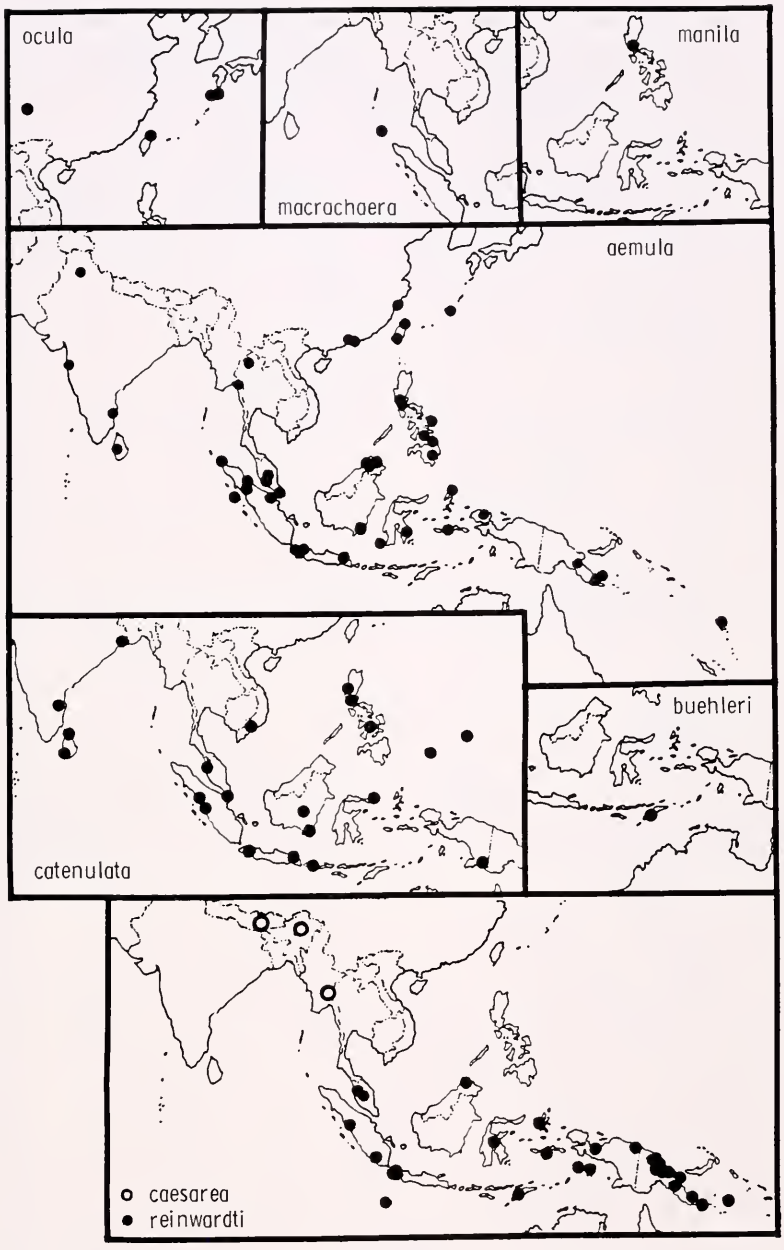
Argiope viabilior Chamberlin, 1924: 16, pl. 4, fig. 32, ♂. Male from N. Gist Gee, Soochow, China, palpi lost, in the U.S. National Museum of Natural History, Washington, examined, is an oxyopid.

Not Recognizable

Argiope manicata Thorell, 1859: 300. Two juvenile specimens from Hong Kong in the Naturhistoriska Riksmuseet, Stockholm labeled "*Argiope tarsalis*" appear to be the types of *A. manicata*. The abdomen ovate to subpentagonal, angular anteriorly, ash gray above, the posterior black. Is this a juvenile specimen of *A. amoena* or perhaps of *A. caesarea*?

Key to Western Pacific Area *Argiope* Females

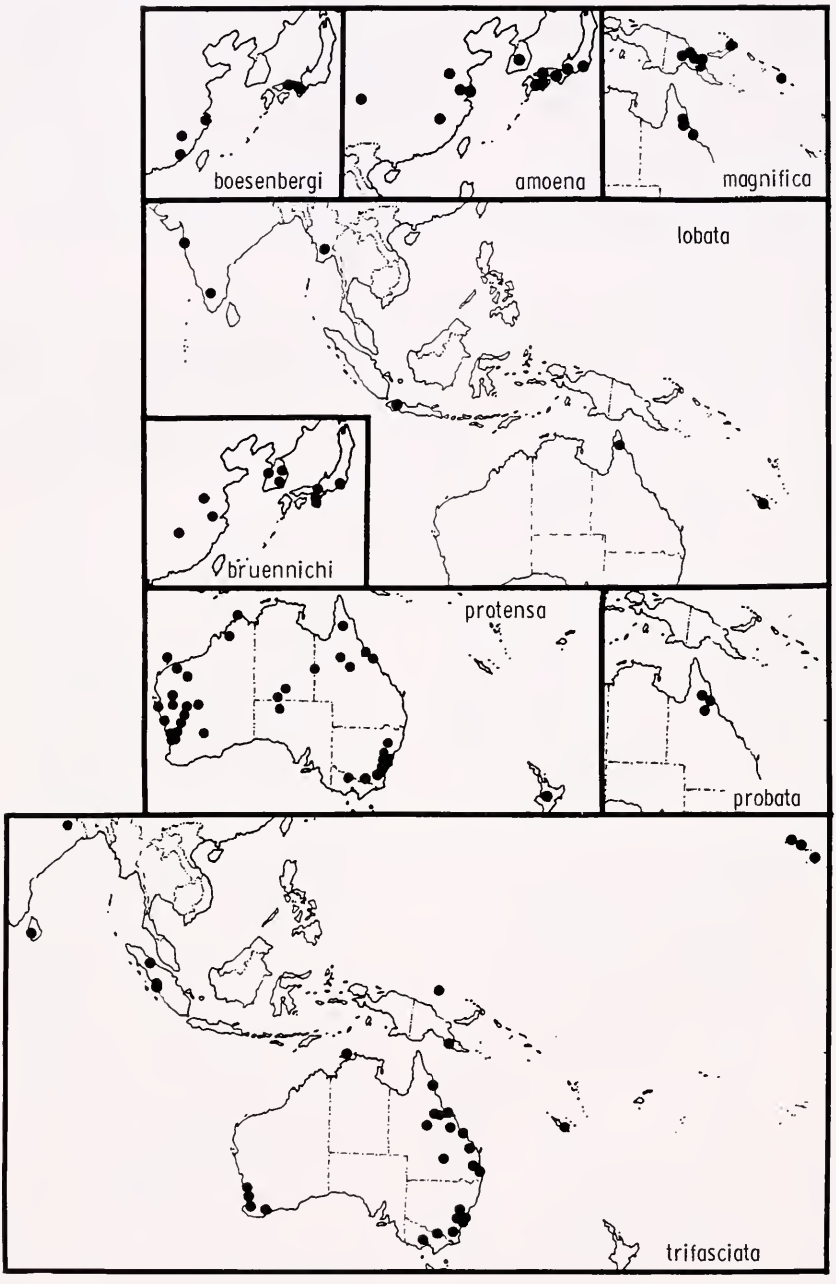
1. Abdomen oval with large lobes all around, as in Figures 93–96; widespread (Map 3) ..... *lobata*
– Abdomen various shapes, without lobes or only shallow lobes 2
2(1). Suboval abdomen with transverse dark lines on dorsum, lines narrower than intermediate light areas (Figs. 33, 78, 84, 115) 20
– Abdomen otherwise 3
3(2). Epigynum with septum constricted anteriorly forming a scape (Figs. 14, 19, 24) 24
– Epigynum without such scape 4
4(3). Abdomen with at least four narrow black and white bands of equal width, posterior on dorsum (Fig. 332); Caroline Islands (Map 5) ..... *ponape*
– Abdomen marked otherwise 5
5(4). Dorsum of abdomen with one to three wide, transverse white bands separated by black bands which on the posterior of the abdomen are about equal width or wider than white bands (Figs. 52, 70, 170, 244, 257); abdomen pentagonal or shield-shaped, widest in middle or in posterior half 26
– Abdomen marked otherwise 6
6(5). Abdomen with a post-spinneret tail (Figs. 102–104, 109, 110) or pointed behind (Figs. 105, 128, 134); New Guinea, Australia, New Zealand 43
– Abdomen rounded behind spinnerets, with at most a slight overhang 7
7(6). Epigynum with anterior edge of rim broken, lateral part of rim narrower than median or lateral part grading into anterior bulge (Figs. 263, 266, 271) 46
– Epigynum with rim entire (Fig. 12) 8
8(7). Abdomen widest posteriorly with a median longitudinal band of white scales breaking transverse black and white marks (Fig. 39); epigynum with thick V-shaped rim and septum; septum width one third that of epigynum (Fig. 36); China, India to New Guinea (Map 2) ..... *catenulata*
– Abdomen marked otherwise; epigynum otherwise 9
9(8). Abdomen shield-shaped, with anterior humps and with a median longitudinal black band constricted anteriorly and a wide white band on each side (Fig. 165); southern China (Map 4) ..... *perforata*
– Abdomen otherwise 10
10(9). Oval abdomen mostly dark except for contrasting yellow or light colored shoulders on dorsum (Figs. 117, 155, 289) 47
– Abdomen marked otherwise 11
11(10). Underside of abdomen with median area white (Figs. 147, 149, 151, 296) 49
– Underside of abdomen with two paraxial white lines enclosing white spots on black 12
12(11). Epigynum trapezoid in outline, as wide as long, widest anteriorly (Fig. 178); septum width half that of epigynum; rims are short anterior arms of septum (Fig. 178); abdomen pentagonal (Fig. 181); Indonesia (Map 4) ..... *niasensis*
– Epigynum otherwise, abdomen sometimes pentagonal 13
13(12). Abdomen shield-shaped with median dorsal light patches framed by black, as in Figure 313; epigynum with posterior lip of opening (on each side of posterior plate) swollen (Fig. 311); Moluccas, New Guinea, northern Australia to Santa Cruz Islands (Map 5) ..... *picta*
– Abdomen marked otherwise; epigynum sometimes with posterior lip of opening swollen 14
14(13). Epigynum longer than wide, rim with long flanges (Fig. 173); abdomen with three pairs of white patches (Fig. 176); Halmahera, New Guinea (Map 4) ..... *halmaherensis*
– Epigynum wider than long 15
15(14). Shield-shaped abdomen with two small anterior nipples and with paired dorsal marks (Fig. 186); venter with two white exclamation marks (Fig. 187); epigynum as in Figures 183, 184, with



Map 2. Distribution of *Argiope ocula*, *A. macrochoera*, *A. manila*, *A. aemula*, *A. catenulata*, *A. buehleri*, *A. caesarea*, and *A. reinwardti*.

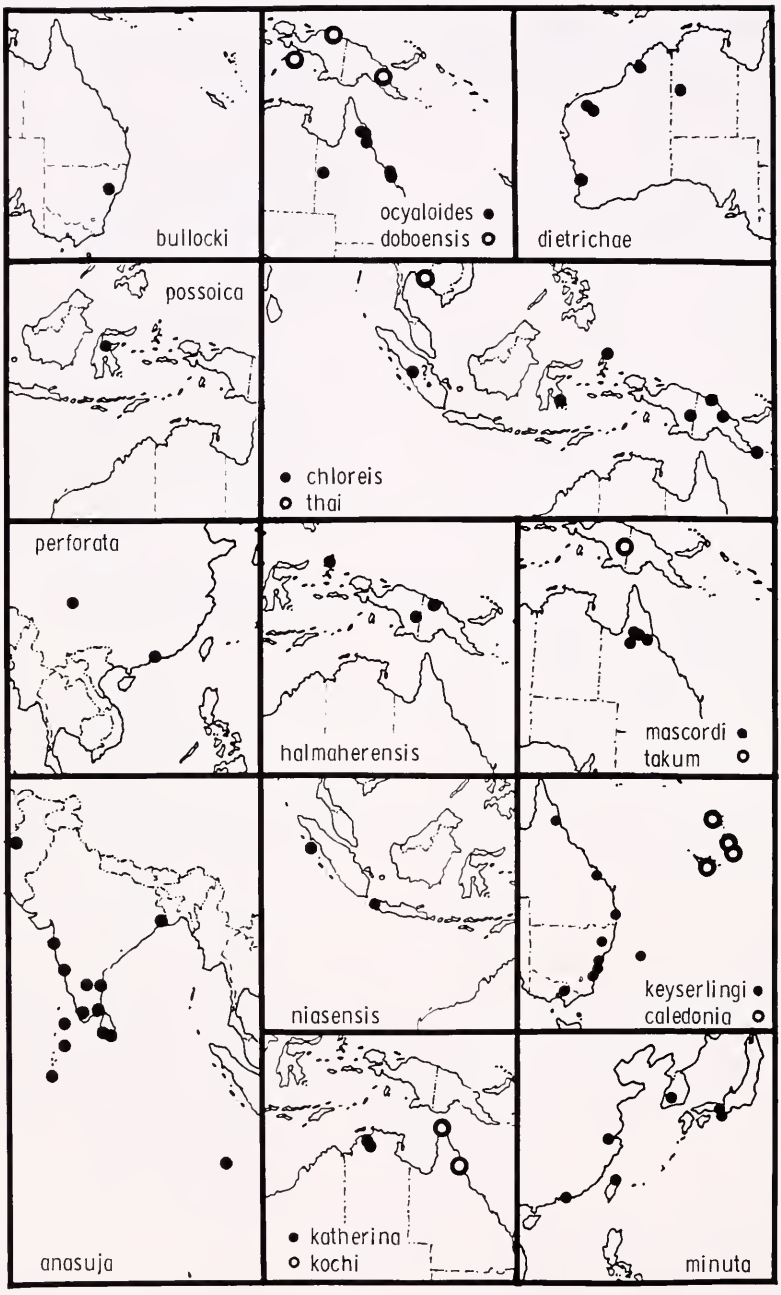
very wide septum and posterior plate; New Guinea (Map 4) ..... *takum*
Abdomen and epigynum otherwise 16

16(15). Abdomen with a dorsal dark folium, lighter on sides or with outline of folium visible in reticulate pattern (Figs. 122, 139, 191, 214) 50
Abdomen marked otherwise 17

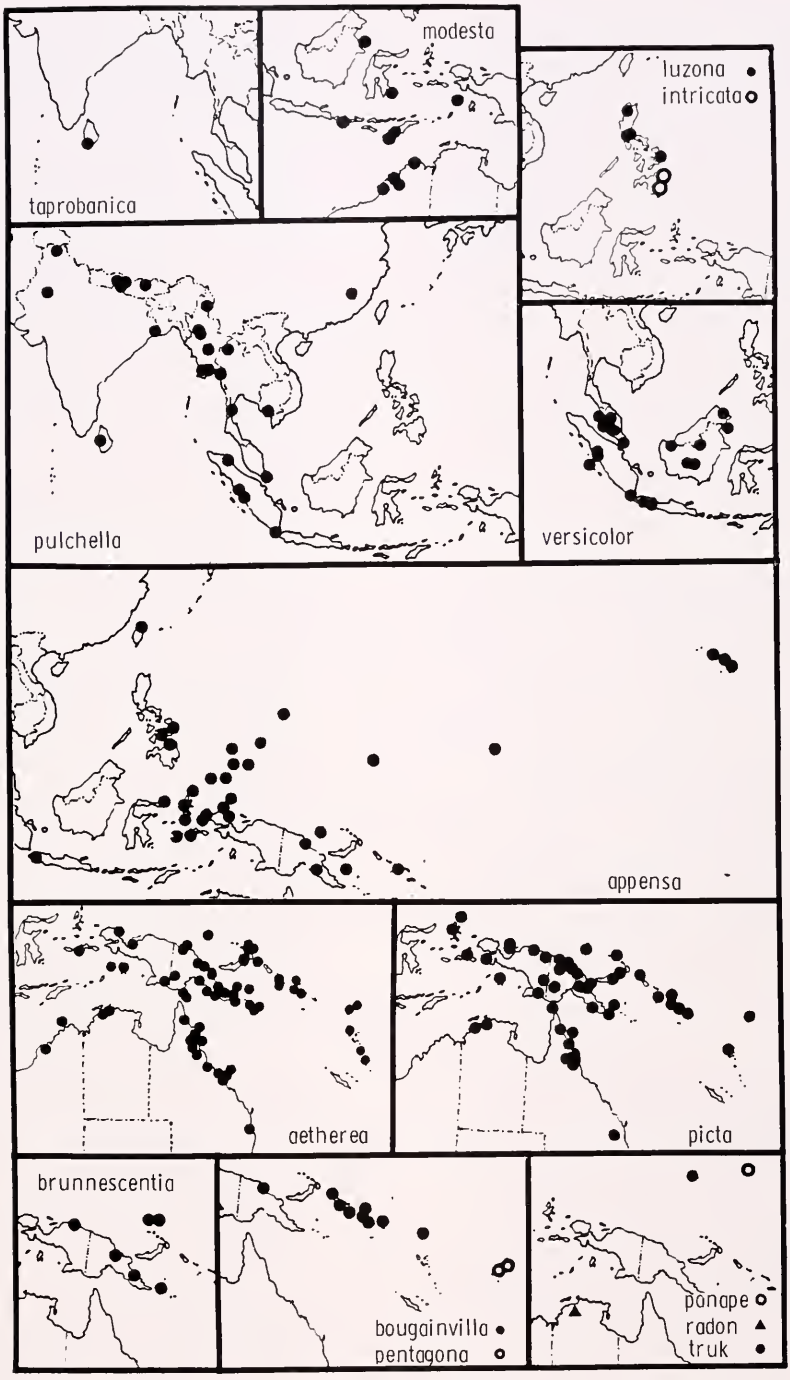


Map 3. Distribution of *Argiope boesenbergi, A. amoena, A. magnifica, A. protensa, A. probata,* and, eastern Asian and western Pacific distributions of *A. bruennichi, A. lobata,* and *A. trifasciata.*

17(16). Center of abdomen dorsum white, silver to yellow sometimes framed by black (Figs. 102, 303, 306, 320); posterior abdominal tip may be black (Figs. 303, 320) 53
– Markings otherwise 18
18(17). Underside of abdomen with two wide, light, longitudinal bands, wider behind than in front and separated by a black band (Fig. 204); dorsum with indistinct transverse bands (Fig. 203); epigynum as in Figures 200–202; northern Australia (Map 4) ..... *kochi*
– Abdomen marked otherwise; epigynum otherwise 19
19(18). Anterior half of pentagonal abdomen light, posterior with a large white patch on each side (Fig. 160); epigynum with rim thicker than septum is wide (Fig. 157); Celebes (Map 4) ..... *possoica*
– Abdomen subcylindrical, with anterior dorsal humps (Fig. 155); epigynum as in Figures 152, 153; Thailand (Map 4) ..... *thai*
20(2). Epigynum with a posterior lobe, containing depression that faces dorsally; lacking septum (Figs. 81–83); Eurasia (Map 3) ..... *bruennichi*
– Depression facing ventrally (Fig. 112) 21
21(20). Septum of epigynum partly bridging rim (Fig. 112); posterior plate filling depression; each side of septum plate hollowed out (Fig. 112); widespread (Map 3) ..... *trifasciata*
– Septum branching anteriorly into the rims (Figs. 29, 73); posterior plate small, not filling depression (Figs. 30, 74) 22
22(21). Underside of pentagonal abdomen with two wide longitudinal bands, wider behind than in front and separated by a black band of equal width (Fig. 204); posterior of dorsum mostly black (Fig. 203); epigynum as in Figures 200–202; northern Australia (Map 4) ..... *kochi*
– Abdomen marked otherwise (Figs. 33, 78); epigynum otherwise (Fig. 29) 23
23(22). Posterior plate of epigynum with median dorsal hump (bottom, Fig. 30); posterior plate covered on sides by lobes of lateral margin (Figs. 30, 31); lateral margins of depression rounded and black on outside (Figs. 29–31); widespread, Asia to New Hebrides (Map 2) ..... *aemula*
– Posterior plate of epigynum with median ventral hump (top, Fig. 77); posterior plate overhanging lateral margins of depression (Figs. 74, 77); lateral margins of depression flat, appearing "unfinished" (Figs. 73, 76); New Guinea, Solomon Islands, Australia (Map 3) ..... *magnifica*
24(3). Abdomen dorsum with transverse bands (Fig. 22); posterior plate with three radiating extensions (Fig. 20); Nicobar Islands (Map 2) ..... *macrochoera*
– Abdomen dorsum with white patches (Fig. 27) or with lateral chevrons (Fig. 16); posterior plate otherwise (Figs. 15, 25) 25
25(24). Abdomen dorsum with white patches (Fig. 27); depressions on each side of scape (Fig. 24); posterior plate longer than wide (Fig. 25); Philippines (Map 2) ..... *manila*
– Abdomen dorsum with lateral chevrons (Fig. 16); epigynal depressions facing posteriorly (Fig. 15); China, Japan (Map 2) ..... *ocula*
26(3). Epigynum longer than wide, rarely square in outline (Figs. 61, 67, 173) 27
– Epigynum wider than long in outline (Fig. 42) 29
27(26). Rims of epigynum with posterior flanges (Fig. 173); Halmahera, New Guinea (Map 4) ..... *halmaherensis*
– Epigynum otherwise 28
28(27). Anterior half of abdomen dorsum light; posterior with a narrow white band on black (Fig. 64); epigynal septum with small anterior groove and lacking anterior bulge (Fig. 61); Japan, China (Map 3) ..... *boesenbergi*
– Abdomen dorsum evenly banded (Fig. 70); epigynal rim U-shaped, surrounding anterior bulge (Fig. 67); Japan, China (Map 3) ..... *amoena*
29(26). Epigynal septum width at least as wide as one fourth width of epigynum (Figs. 42, 47, 56) 30
– Septum width less than one quarter of epigynum (Figs. 157, 200) 33
30(29). Depression of epigynum bordered by rim laterally in ventral view and containing posterior plate (Fig. 222); posterior plate wider than septum (Fig. 223); Sri Lanka (Map 5) ..... *taprobanica*
– Depression in ventral view not bordered laterally by rim (Figs. 42, 47); posterior plate as wide as septum (Figs. 43, 48) 31
31(30). Epigynum with septum round, appearing swollen (Fig. 42); Timor (Map 2) ..... *buehleri*
– Epigynum flattened posteroventrally (Figs. 47, 56) 32
32(31). Sternum yellowish with gray around edge (Fig. 53); rims of epigynum lat-



Map 4. Distribution of *Argiope bullocki, A. doboensis, A. ocyaloides, A. dietrichae, A. possoica, A. chloreis, A. thai, A. perforata, A. halmaherensis, A. mascordi, A. takum, A. anasuja, A. niasensis, A. caledonia, A. keyserlingi, A. katherina, A. kochi,* and *A. minuta.*



Map 5. Distribution of *Argiope taprobanica*, *A. modesta*, *A. intricata*, *A. luzona*, *A. pulchella*, *A. versicolor*, *A. appensa*, *A. aetherea*, *A. picta*, *A. brunnescentia*, *A. bougainvilla*, *A. pentagona*, *A. ponape*, *A. radon*, and *A. truk*.

erally wide (Fig. 47); Malay Peninsula, Borneo, Indonesia, New Guinea (Map 2) ..... *reinwardti*

– Sternum black with median light longitudinal band (Fig. 60); rims of epigynum narrowing laterally (Fig. 56); northeastern India, Burma (Map 2) ..... *caesarea*

33(29). Underside of abdomen with two longitudinal bands as wide as intermediate area (Fig. 204); northern Queensland (Map 4) ..... *kochi*

– Underside of abdomen with two narrow longitudinal lines 34

34(33). Epigynal rim much thicker than septum width (Fig. 157); Celebes (Map 4) ..... *possoica*

– Epigynal rim as thick as septum width or narrower (Figs. 167, 194, 205) 35

35(34). Rims of epigynum with transverse flange, posterior edge flange straight, at right angles to axis of septum (in ventral view) (Figs. 167, 205) 36

– Rims, flange if present, and epigynal depression otherwise (Fig. 194) 37

36(35). Flanges of rim with a tooth on each side (Fig. 167); Pakistan, India, Cocos Keeling Islands (Map 4) ..... *anasuja*

– Flanges enclosing posterior plate laterally (Fig. 205); Japan, China (Map 4) ..... *minuta*

37(35). Epigynum in posterior view with circular opening in depression (Figs. 195, 218); Australia, New Caledonia 38

– Epigynum otherwise 39

38(37). Epigynum in ventral view with a lobe on each side of posterior plate (Fig. 194); epigynum rectangular in outline in posterior view (Fig. 195); east coast of Australia (Map 4) ..... *keyserlingi*

– Epigynum without lobes on each side of opening (Figs. 217, 218); epigynum rounded in outline in posterior view (Fig. 218); New Caledonia (Map 4) ..... *caledonia*

39(37). Anterior bulge of epigynum very large, almost hiding posteriorly- or laterally-facing depressions (Figs. 238, 251, 254); Asia, Borneo, Indonesia 40

– Anterior bulge of usual size (Figs. 227, 233); Philippines, Moluccas to Australia 41

40(39). Anterior bulge rectangular to oval, wider than long; depressions facing posteriorly (Figs. 251, 253, 254, 256); depressions containing large piece of palpal embolus (Figs. 261, 262); Borneo, Malay Peninsula to Java (Map 5) ..... *versicolor*

– Anterior bulge subcircular, depressions facing posterolaterally (Figs. 238, 240, 241, 243); depressions containing small tip of embolus (Fig. 250); India, Malay Peninsula to Java (Map 5) ..... *pulchella*

41(39). Epigynum with narrow septum widening abruptly into posterior plate (Fig. 228); in posterior view depression framed by set-off rim (Fig. 228); northern Philippines (Map 5) ..... *luzona*

– Epigynum with septum gradually widening into posterior plate (Figs. 233, 297); in posterior view depression not framed by distinct rim (Figs. 234, 298) 42

42(41). Epigynum with posterior plate slightly lobed, its width more than one third that of epigynum (Fig. 234); lips of depression curved (Fig. 233); sternum maculated (Fig. 237); southern Philippines (Map 5) ..... *intricata*

– Epigynum with posterior plate edges straight and its width narrower (Fig. 298); lips of opening within depression straight; sternum usually bright yellow (Fig. 304); Ambon, New Guinea, Solomon Islands, New Hebrides, northern Australia (Map 5) ..... *aetherea*

43(6). Epigynum a median posterior lobe containing depressions which face dorsally (Figs. 98–101); Australia, New Zealand (Map 3) ..... *protensa*

– Epigynum with depressions facing ventrally (Fig. 107); New Guinea, northeastern Australia 44

44(43). Anterior of abdomen rounded (Fig. 109), light colored with a median dorsal abdominal dark mark (Fig. 109); northeastern Australia (Map 3) ..... *probata*

– Anterior of abdomen lobed or pointed on each side; dark colored with paired longitudinal marks or folium (Figs. 127, 133) 45

45(44). Abdomen lobed anteriorly (Fig. 127); epigynal rim and septum forming T (Fig. 124); Australia (Map 4) ..... *ocyaloides*

– Abdomen with anterior points (Fig. 133); epigynal septum and posterior plate forming an upside-down T (Fig. 130); New Guinea (Map 4) ..... *doboensis*

46(7). Abdomen with shallow lobes all around, pentagonal in outline (Figs. 269, 270); epigynum ventrally drawn out (Figs. 265, 268); Borneo to northwestern Australia (Map 5) ..... *modesta*

– Abdomen only slightly lobed behind with characteristic reticulate pattern more distinct around edge (Figs. 274–276); epigynum not ventrally drawn out (Fig. 273); Hawaii, southern Japan, Taiwan to Java, New Guinea, Solomon Islands (Map 5) ..... *appensa*

47(10). Epigynal septum bridging rim in part (Fig. 112); Kauai Island of Hawaii (Map 3) ..... *trifasciata*
– Epigynum otherwise (Fig. 286) 48
48(47). Abdomen without humps, widest anteriorly (Fig. 289); Solomon Islands (Map 5) ..... *bougainvilla*
– Abdomen with humps, widest in posterior (Fig. 155); Thailand (Map 4) ..... *thai*
49(11). Abdomen pentagonal in outline (Fig. 295); ventral white area wider than long, with eight arms (Fig. 296); Fiji (Map 5) ..... *pentagona*
– Abdomen shield-shaped (Figs. 146, 150); ventral white area longer than wide (Figs. 147, 149); Sumatra to New Guinea (Map 4) ..... *chlorcis*
50(16). Epigynal depression laterally surrounded by rim; septum flaring into depression (Fig. 120); New South Wales (Map 4) ..... *bullocki*
– Epigynal depression not laterally surrounded by rim; or, if surrounded, septum a discrete structure (Fig. 136) 51
51(50). Posterior plate of epigynum only slightly wider than septum; in posterior view circular openings visible (Fig. 189); Queensland (Map 4) ..... *mascordi*
– Posterior plate of epigynum much wider than septum (Figs. 137, 212) 52
52(51). In posterior view rim surrounds depressions and circular openings are visible (Fig. 212); Northern Territory (Map 4) ..... *katherina*
– Openings on each side under a curved slit within the depression (Fig. 136); Western Australia, Northern Territory (Map 4) ..... *dietrichae*
53(17). Elongate abdomen silvery with only faint longitudinal dorsal marks (Fig 102); epigynum a posterior lobe containing depressions that face dorsally (Figs. 98–101); New Zealand, Australia (Map 3) ..... *protensa*
– Abdomen various shapes (Figs. 303, 320), usually darker around dorsal edge (Figs. 303, 327); epigynal depressions facing ventrally (Figs. 297, 317) 54
54(53). Abdomen pentagonal, bulging, with only V-shaped marks around margin (Fig. 282); New Guinea, Bismarck Archipelago (Map 5) ..... *brunnescentia*
– Abdomen otherwise 55
55(54). Abdomen elongate, shield-shaped, slightly constricted behind humps (Fig. 320); Northern Territory (Map 5) ..... *radon*
– Abdomen pentagonal or oval 56
56(55). Abdomen pentagonal, usually posterior tip black (Fig. 303); Moluccas to New Hebrides, northern Australia (Map 5) ..... *aetherea*
– Abdomen oval (Fig. 327); Caroline Islands (Map 5) ..... *truk*

KEY TO WESTERN PACIFIC AREA MALE *ARGIOPE*

The males of a number of species are unknown: *buehleri, bullocki, caledonia, caesarea, chlorcis, dietrichae, halmaherensis, intricata, macrochoera, manila, modesta, niasensis, pentagona, perforata, ponape, possoica, takum, taprobanica, thai,* and *truk.*

There is some doubt as to whether the following have been correctly matched: *brunnescentia, kochi,* and *mascordi.*

1. A distal kink on the embolus' outer ("upper") surface (Fig. 13) 19
– Upper surface of embolus without kink, at most slightly twisted (Figs. 35, 41, 80) 2
2(1). In mesal view the tegulum surrounds short embolus and conductor (Figs. 35, 41, 54, 199) 24
– Embolus and conductor extend beyond tegulum (Figs. 66, 80, 106) 3
3(2). Embolus forms a circle on ventral surface as in Figure 119; widespread (Map 3) ..... *trifasciata*
– Embolus not a coil on ventral surface (Figs. 72, 111) 4
4(3). Embolus coiled back on itself (Figs. 111, 129); Australia 27
– Embolus straight, curved, or coiled, not doubled up on itself (Figs. 54, 72) 5
5(4). Embolus curved with a slight twist in middle as in Figures 248, 259 6
– Embolus otherwise (Figs. 106, 232) 7
6(5). Pendant longer than embolus tip (Fig. 248); India to Java (Map 5) ..... *pulchella*
– Pendant shorter than embolus tip (Fig. 259); Malay Peninsula to Java, Borneo (Map 5) ..... *versicolor*
7(5). Embolus very long and conductor hanging "down" (Fig. 106); Australia, New Zealand (Map 3) ..... *protensa*
– Embolus of usual length and conductor directed straight out at 45° angle from axis of palpus (Figs. 97, 232) 8
8(7). Embolus arched, its tip held by a bowl-shaped conductor as in Figure 232; northern Philippines (Map 5) ..... *luzona*
– Embolus and conductor otherwise (Figs. 97, 210, 216) 9
9(8). Embolus with a terminal twist, its tip hidden by conductor in mesal view (Figs. 210, 216) 28
– Embolus without distal twist (Fig. 97) 10
10(9). Two barbs on base of embolus (Fig. 97); widespread (Map 3) ..... *lobata*
– Embolus without barbs (Fig. 18) 11

11(10). Embolus with a blunt spur on "upper" side; median apophysis with thorn-shaped spur (Fig. 18); Japan, China (Map 2) ..... *ocula*

– Embolus without spur (Fig. 54); median apophysis spur filamentous 12

12(11). Embolus with a much wider, set-off base (Figs. 54, 55); Malay Peninsula, Borneo, Indonesia to New Guinea (Map 2) ..... *reinwardti*

– Embolus evenly tapered (Figs. 66, 72) 13

13(12). Base of embolus near edge of tegulum (Figs. 66, 193); embolus length about equal that of previous sclerite (Figs. 66, 193) 14

– Base of embolus closer to edge of cymbium (Figs. 72, 86); embolus length much longer than previous sclerite 15

14(13). Proximal embolus sclerite butting against previous sclerite (Fig. 193); Queensland (Map 4) ..... (?) *kochi* or *mascordi*

– Proximal embolus sclerite overlapped by previous sclerite (in part hidden by edge of cymbium) (Fig. 66); Japan, China (Map 3) ..... *boesenbergi*

15(13). Base of embolus flaring, overhanging proximal sclerite; spur originating from inner corner of bend of median apophysis (Fig. 72); Japan, China (Map 3) ..... *amoena*

– Base of embolus butting against proximal sclerite without overhang; spur originating on face of median apophysis or near tip (Figs. 86, 135) 16

16(15). Embolus evenly arched as in Figure 135; spur near tip of median apophysis (Fig. 135); New Guinea (Map 4) ..... *doboensis*

– Embolus only gently curved or only distal portion bent; spur originating from face of median apophysis near bend (Fig. 86) 17

17(16). Median apophysis spur much longer than two diameters of median apophysis (Fig. 86); Eurasia (Map 3) ..... *bruennichi*

– Median apophysis spur shorter (Figs. 80, 172) 18

18(17). Embolus distally strongly curved (Fig. 172); Pakistan, India, Cocos Keeling Islands (Map 4) ..... *anasuja*

– Embolus with only slight bend (Fig. 80); New Guinea, Australia (Map 3) ..... *magnifica*

19(1). Median apophysis spur on lower edge of very tip (Fig. 315); Moluccas, New Guinea, northern Australia to Santa Cruz Islands (Map 5) ..... *pieta*

– Spur attached to "upper" surface near bend (Figs. 277, 291, 308) 20

20(19). Median apophysis spur on upper surface near distal end (in mesal view) (Fig. 308); Moluccas to New Hebrides, northern Australia (Map 5) ..... *aetherea*

– Median apophysis attached to outer surface or near bend (Figs. 277, 284) 21

21(20). Median apophysis spur attached on outer surface near tip (Figs. 277, 291) 22

– Median apophysis spur attached on outer surface near bend (Figs. 284, 322) 23

22(21). Upper surface of embolus with two crests near tip (Fig. 277); Hawaii, southern Japan, Taiwan to Java, New Guinea, Solomon Islands (Map 5) ..... *appensa*

– Upper surface without such crests (Fig. 291); Solomon Islands (Map 5) ..... *bougainvilla*

23(22). Pendant overlapping embolus tip (Fig. 322); Northern Territory (Map 5) ..... *radon*

– Pendant separated from embolus tip (Fig. 284); New Guinea, Bismarck Archipelago (Map 5) ..... *brunnescentia*

24(2). Embolus a heavily sclerotized prong as in Figures 54, 55; Malay Peninsula, Borneo, Indonesia to New Guinea (Map 2) ..... *reinwardti*

– Embolus a different structure (Figs. 35, 41, 199) 25

25(24). Embolus a large curved structure with a truncate branch on its lower side from base and a notch near tip as in Figure 199; eastern coast of Australia (Map 4) ..... *keyserlingi*

– Embolus otherwise (Figs. 35, 41) 26

26(25). Conductor fan-shaped; a sclerotized truncate tip on upper branch of complex conductor (Fig. 41); China, India to New Guinea (Map 2) ..... *eatenulata*

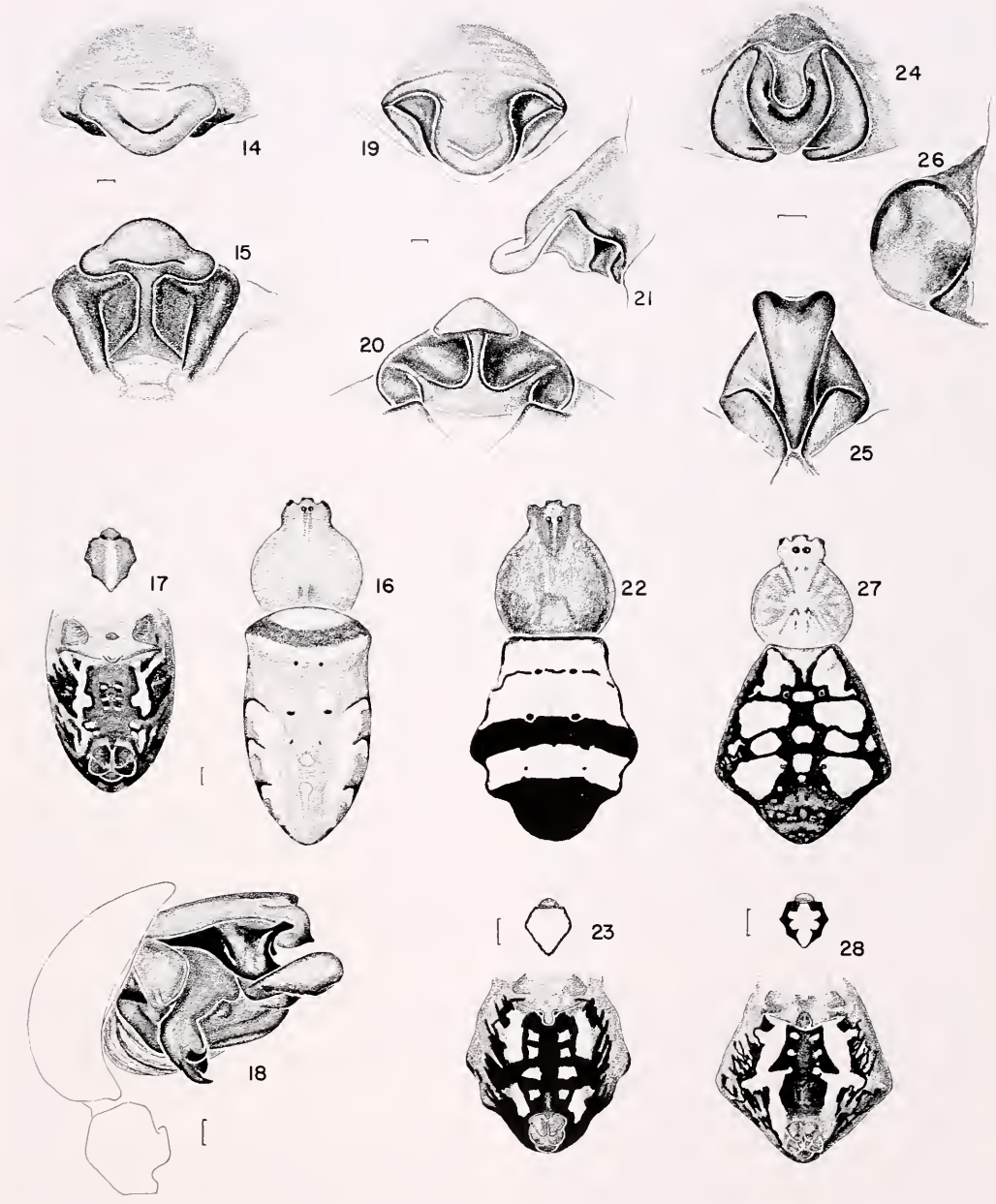
– Conductor a heavily sclerotized lobe; embolus sclerotized, with a seam across its middle and a curved tip as in Figure 35; widespread, Asia to New Hebrides (Map 2) ..... *aenula*

27(4). Embolus with pendant; one branch of median apophysis long; spur attached on upper surface (Fig. 111); Queensland (Map 3) ..... *probata*

– Embolus without pendant, two branches of median apophysis of equal length and diverging; spur attached to lower surface (Fig. 129); Queensland (Map 4) ..... *ocyaloides*

28(9). Embolus heavy and with a base; inner branch of median apophysis hidden by outer one (Fig. 216); Queensland (Map 4) ..... *katherina*

– Embolus slender without a base; inner branch of median apophysis hanging "down" (Fig. 210); Japan, China (Map 4) ..... *minuta*



Figures 14–18. *Argiope ocula* Fox. 14–17. Female. 14. Epigynum, ventral. 15. Epigynum, posterior. 16. Carapace and abdomen. 17. Sternum and abdomen. 18. Left male palpus, mesal.

Figures 19–23. *Argiope macrochoera* Thorell, female. 19. Epigynum, ventral. 20. Epigynum, posterior. 21. Epigynum, lateral. 22. Carapace and abdomen. 23. Sternum and abdomen.

Figures 24–28. *Argiope manila* n. sp., female. 24. Epigynum, ventral. 25. Epigynum, posterior. 26. Epigynum, lateral. 27. Carapace and abdomen. 28. Sternum and abdomen.

Scale lines. 0.1 mm, except Figures 16, 17, 22, 23, 27, 28, 1.0 mm.

Argiope ocula Fox

Figures 14–18; Map 2

Argiope ocula Fox, 1938: 364, fig. 6, ♀. Female holotype from Shin-Kai-Si, Mount Omi [O-Mei San] (1200–1500 m), Szechwan, China in the U.S. National Museum, examined.

Argiope ohsumiensis Yaginuma, 1967: 50, figs. 1–9, ♀, ♂. Female holotype from Kurio, Yaku Island [Yaku Shima], Japan, 1 Aug. 1961 in the collection of the Arachnological Society of East Asia, examined. 1971: 128, fig. 107: 12–17, ♀♂. NEW SYNONYMY.

Notes. Superficially this species does not appear to resemble an *Argiope*. But the posterior eye row is slightly procurved and the posterior lateral eyes have a narrow tapetum, as do *Argiope* (but not *Araneus*). The carapace shape is *Argiope*-like with a narrow head and a pair of comma-shaped marks behind the thoracic depressions, as found in other *Argiope* species (Fig. 16).

The male has none of the coxae modified, nor do the legs have heavier macrosetae than the female's. There is a broad, indistinct tooth lateral on the endites, but none facing it on the palpal femur. The embolus is thorn-shaped with a broad base, its pointed tip hidden by the conductor (Fig. 18). The tip breaks off when mating as in other species and is found stuck in the depression of the epigynum. The male from Taiwan has both emboli missing; it survived mating.

Diagnosis. This is the only *Argiope* with a distinct *Araneus*-like scape in the epigynum (Fig. 14). The shape and markings of the thick abdomen, with anterior dorsal humps and pointed posterior (Fig. 16), are diagnostic. The axis of the male's median apophysis is at an obtuse angle to that of the conductor, and its spur is thorn-shaped (Fig. 18).

Variation. Females differ in the shape of the opening in the depression. The Taiwan specimens are more like the type of *A. ocula* than the specimens from Japan illustrated (Figs. 14, 15).

Records. JAPAN: Nakatane-ono, Tane Isl., 22 July 1963, ♂ (H. Ohe, ASEA); Kagoshima, Tanegashima Isl., 22 July 1965, ♀ (H. Ohe, ASEA); 23 July 1971, ♀ (T. Yaginuma, ASEA). TAIWAN: *Tai Pei County.* Wulai, 6 July 1977, ♀♂ (H. Yoshida, YC); Yangmingshan, 2 Aug. 1977, ♀ (H. Yoshida, YC).

Argiope macrochoera Thorell

Figures 19–23; Map 2

Argiope macrochoera Thorell, 1891: 50. Two females, two juvenile syntypes from Nicobar Islands [Bengal Bay, Indian Ocean], in the Zoologisk Museum, Copenhagen, examined. Roewer, 1942: 738. Bonnet, 1955: 691.

Diagnosis. Like *A. manila*, the rim and septum are formed into a scape-like structure constricted anteriorly (Fig. 19). *Argiope macrochoera* differs by having the abdomen banded, and, in posterior view, the posterior plate of the epigynum is wider than long and appears to have three branches (Fig. 20), the middle one being the septum.

Argiope manila new species

Figures 24–28; Map 2

Holotype. Female and four female paratypes from Luzon, Philippines, most legs broken. Holotype and three paratypes in the Senckenberg Museum, Frankfurt, and one in the Museum of Comparative Zoology. The specific name is a noun in apposition after the type locality.

Description. Carapace yellow-white with indistinct darker marks. Sternum with bright yellow-white branched mark surrounded by black (Fig. 28). Legs brown, not banded. Dorsum of abdomen with light patches on black (Fig. 27). Venter marked as usual (Fig. 28). Anterior lateral eyes 0.5 diameter of others, which are subequal. Anterior median eyes 0.8 diameter apart, 1.2 from laterals. Posterior median eyes slightly more than their diameter apart, 1.8 from laterals. The abdomen is pentagonal. Total length, 11.5 mm. Carapace, 4.7 mm long, 4.2 mm wide. First femur, 8.2 mm; patella and

tibia, 8.6 mm; metatarsus, 8.6 mm; tarsus, 2.0 mm. Second patella and tibia, 8.6 mm; third, 4.5 mm; fourth, 7.2 mm.

Diagnosis. This species differs from all others by the distinct abdominal markings (Fig. 27) and by the unusual shape of the epigynum: the rim and the septum form a scape-like structure, constricted anteriorly (Fig. 24). The lateral margins of the depressions are rounded, dark on the outside (Fig. 24), and the posterior plate is like that of *Argiope aemula*.

Argiope aemula (Walckenaer)

Figures 29–35; Map 2

Epeira aemula Walckenaer, 1841: 118. Specimens from Celebes, lost.

Epeira striata Doleschall, 1857: 415. Name given to illustration of specimens from Java. Two original specimens here labeled syntypes in the Rijksmuseum van Natuurlijke Historie, Leiden, examined.

Argiope aemula:—Thorell, 1877: 364. Roewer, 1942: 739 (in part). Bonnet, 1955: 670 (in part). Song, 1980: 100, fig. 46, ♀.

Argiope aemula nigripes Thorell, 1877: 364. Female holotype from Kondari [Kendari], Celebes in the Museo Civico di Storia Naturale, Genova, examined.

Argiope trivittata Karsch, 1891: 280, pl. 10, fig. 6, ♀. Female holotype from Ceylon [Sri Lanka] in the Zoologisches Museum, Humboldt Universität, Berlin, examined.

Metargiope ornatus var. *lineatus* Marapao, 1965: 46, pl. 2, ♀. Female holotype from Tipolo, Mandawe, Cebu, Philippines in the Univ. San Carlos, Cebu City, not available. NEW SYNONYMY.

Argiope sp. "Wau no. 5" M. H. Robinson and B. Robinson, 1980: 10, 50, 82–85, 89, 192, figs. 37–38, ♀, ♂ (photo).

Argiope sp. "Singapore no. 1" M. H. Robinson and B. Robinson, 1980: 10, 50, 88–91, 192, fig. 42, ♂ (photo).

Note. Several specimens of this species from Celebes, the type locality, were examined. Chrysanthus (1971), B. Robinson and M. H. Robinson (1974), M. H. Robinson, Y. D. Lubin, and B. Robinson (1974), and M. H. Robinson and B. Robinson (1980) misidentified *A. aemula*. Their specimens were *A. magnifica* L. Koch, a superficially similar species. Figures 29, 30, 32–34 were made from a specimen from Bulolo, Papua New Guinea, Figure 31 from Bombay, India, and Figure 35 from Malaysia. Specimens from Bombay, India have the lateral margins of the depressions of the epigynum swollen posteriorly (Fig. 31).

Diagnosis. This is one of the largest species of *Argiope*, females often more than 20 mm total length. The oval abdomen is slightly truncate anteriorly, with indistinct shoulder humps and is dorsally marked with transverse lines (Fig. 33). The epigynum differs from that of *A. magnifica*, a similar species, by having a posterior median swelling on the posterior plate (Figs. 30, 31), also visible in ventral view. The lateral borders of the depression are smooth, rounded and seemingly polished, the outside edge black (Figs. 29, 32). In posterior view the lateral borders end in large lobes (Figs. 30, 31). The epigynum is similar to that of *A. catenulata*, which is a smaller species and has very different markings on the abdomen: dorsally a longitudinal band of white setae, and on the venter a transverse white mark connecting the longitudinal white lines.

The male palpus in mesal view has a short embolus and conductor, and a complex median apophysis surrounded by a large tegulum (unlike most *Argiope* males). The embolus has a seam where it perhaps breaks off in mating; the tip is a sclerotized hook held by a short, straight conductor (Fig. 35).

Natural History. Specimens were found in cow pastures and on roadside vegetation near Binatang Creek in the Wau Valley, Papua New Guinea, among populations of *A. magnifica*. The web has a cruciform stabilimentum. Courtship and mating are reported in M. H. Robinson and B. Robinson, 1980. Of interest are the behavioral differences reported by Robinson and Robinson between the populations from Singapore and those from New Guinea ("Wau no. 5" and "Singapore no. 1").

Distribution. Japan, India to Indonesia and New Hebrides (Map 2).

Records. JAPAN: *Nansei Islands.* Okinawa (many records, MCZ, AMNH); "Japan," (NMW). TAIWAN: Tai Pei (AMNH); Takao (NMW). CHINA: (Song, 1980); Fumni [? Funing] (ZMB); Canton (SMF). HONG KONG: (NMW, SMF). THAILAND: Doi Inthanon Natl. Park, Chieng Mai Prov., 14 Oct. 1981 (ZMK). SINGAPORE: (MCZ, BMNH). MALAYSIA: *Malay Peninsula.* Jokor Layang-Layang, jungle remnant (MC); Fraser's Hill, 1300 m (CAS); Bukit Tima (MCZ); Pahang (ZRC). *Sarawak.* Gunong Mulu Natl. Park, in grass on bank of Melinau River (BMNH). *Sabah.* Ulu Dusun, nr. Sandakan (MC); Manutek Isl., Kota Kinabalu, in grass (MC); Kudat (ZRC); Bundu Tuan (ZRC). BURMA: Mulmein (NMW). INDIA: *Punjab.* Amballa [Umballa] (MCZ). *Assam.* Chabua (AMNH). *Madras.* Vellore (ZMK). *Maharashtra.* Bombay (SMF). PHILIPPINES: *Calicoan and Lebanon Isls.* (AMNH); Santa Clara, above Gingo-og (FMC); Samar Isl. (AMNH). *Luzon.* Quezon City (AMNH); Subic (CAS); Alabang, Rizal Prov. (AMNH, ZMB); Manila (MNHN, IRSN, ZMB). *Mindanao.* Davao Prov. (MCZ); Butuan (MCZ). INDONESIA: *Sumatra.* E of Langkai Isl. (MCZ); between Taroengen [Tarutung] and Bircuen (MCZ); Nias Isl. (ZMK, BMNH); Pulau Weh Isl. (BMNH); Fort de Kock [Bukittinggi], 920 m (SMF); Bungar-Bondar [West Sumatra] (SMF); West Sumatra (BMNH); Medan (NMW). *Java.* Batavia [Djakarta] (MCZ); Buitenzorg [Bogor] (MCZ); Bantar Gebang (MCZ); Tjibodas [Cibodas] (NMW); Tengger Mts. (ZMB). *Southeast Borneo* [Kalimantan]. Tandjong (ZMH); Pagat [Pagatan] (ZMB). *Moluccas.* Celebes: Toli-Toli (MCZ); Kendari (MCSN). Halmahera: Morotai (AMNH). Ceram: Amboina [Ambon] (BMNH). WEST IRIAN: [Djaya Pura]. Manapi, Cape Vogel Penins. (AMNH). PAPUA NEW GUINEA: *Northern Distr.* Oro Bay, 1945, ♀ (S. Sandler, AMNH). *Milne Bay Distr.* Goodenough Isl., 1943, ♀ (W.B. Jones, AMNH). *Morobe Distr.* Bulolo, 17 March 1979, ♀ (M. Robinson, H. Levi, *et al.*, MCZ); Oomsis, April 1959, ♀ (J. Gunn, AMNH). NEW HEBRIDES: Aore Isl., April 1944, ♀ (W.L. Nutting, MCZ).

Argiope catenulata (Doleschall)

Figures 36–41; Map 2

Epeira catenulata Doleschall, 1859: 30, pl. 9, fig. 1, ♀. Name given to illustration of specimens from Java in the Rijksmuseum van Natuurlijke Historie, Leiden, which were examined.

Argiope opulenta Thorell, 1859: 299. Female from Java in the Naturhistoriska Riksmuseet, Stockholm, not examined.

Epeira (Argiope) stellata Stoliczka, 1869: 234, pl. 28, fig. 6, ♀. Female from Sundarbans, south of Port Canning, India, not examined.

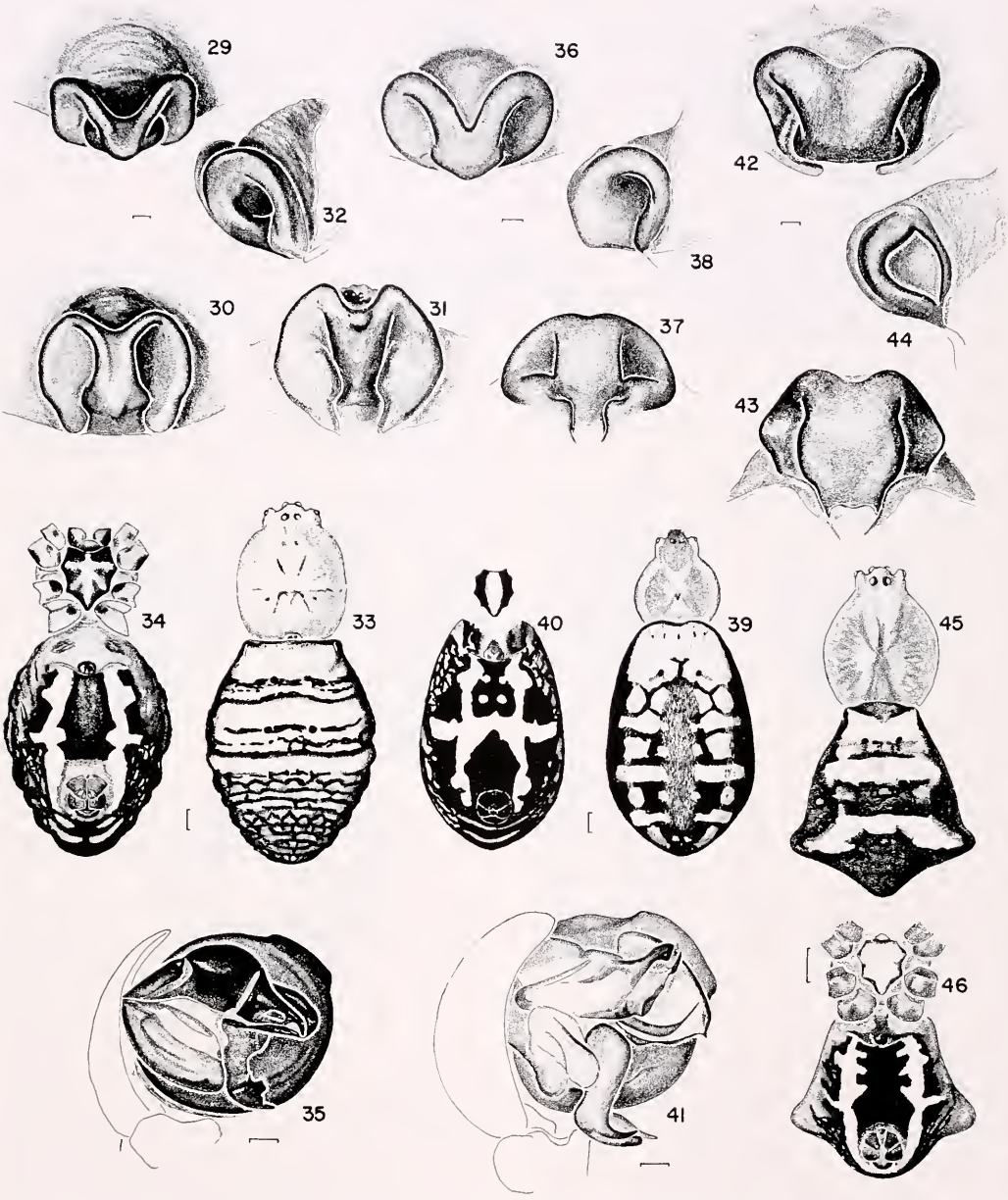
Argiope pelewensis Keyserling, 1886: 136, pl. 11, fig. 2, ♀. Female holotype from Pelew Inseln [Palau, Caroline Islands] in the Zoologisches Museum, Universität Hamburg, examined.

Argiope catenulata:—Roewer, 1942: 741. Bonnet, 1955: 683. Chrysanthus, 1958: 240, figs. 13–18, 22, ♀, ♂. Song, 1980: 101.

Metargiope ornatus var. *turricula* Marapao, 1965: 47, pl. 3, ♀, ♂. Female holotype from Cebu City, Philippines on tall grasses on vacant lot in the San Carlos Univ., Cebu City, unavailable. NEW SYNONYMY.

Note. Stoliczka's illustration shows the diagnostic coloration. Simon synonymized *Pronous chelifer* Hasselt (1882) with this species; this is an error; it is *Gea spinipes.* The illustrations (Figs. 36–40) of the female were made from a Philippine specimen, that of the male palp (Fig. 41) the mirror image of a right palpus of a specimen from Sumatra. Because of the setal covering of the abdomen, I expect living specimens to have a slightly different pattern from that of the one illustrated.

Diagnosis. Unlike other species, the abdomen is oval, widest in the posterior half, with a unique black and white dorsal pattern. The midline is covered in a longitudinal band of white setae (Fig. 39, in alcohol). The venter has a diagnostic transverse white band (Fig. 40). The epigynum is much like that of *A. aemula*, with a wide septum, the lateral border of the depression curved and dark along the outer edge (Figs. 36, 37).



Figures 29–35. *Argiope aemula* (Walckenaer). 29–34. Female. 29. Epigynum, ventral. 30, 31. Epigynum, posterior. 29, 30, 32. (Papua New Guinea). 31. (India). 32. Epigynum, lateral. 33. Carapace and abdomen. 34. Sternum and abdomen. 35. Left male palpus, mesal.

Figures 36–41. *Argiope catenulata* (Doleschall). 36. Epigynum, ventral. 37. Epigynum, posterior. 38, Epigynum, lateral. 39. Carapace and abdomen. 40. Sternum and abdomen. 41. Left male palpus, mesal.

Figures 42–46. *Argiope buehleri* Schenkel, female. 42. Epigynum, ventral. 43, Epigynum, posterior. 44. Epigynum, lateral. 45. Carapace and abdomen. 46. Sternum and abdomen.

Scale lines. 0.1 mm, except Figures 33, 34, 39, 40, 45, 46, 1.0 mm.

The male has an evenly curved embolus containing a fine duct held by the conductor and partly hidden by an elaborate stipes (Fig. 41), quite distinct from that of other species.

Distribution. China (Song, 1980), India, Indonesia, Philippines to New Guinea (Map 2).

Records. INDIA: *Madras.* Vellore, ♀ (N. Löwenthal, ZMK). SRI LANKA (CEYLON): 1864, ♀ (Sarasin, ZMB); Kejkant ved Balangoda [Balangoda], 12 April 1957, juv. (Galathea Exp., ZMK). VIETNAM: Saigon, 1966–1967, juv. (P. Fleischer, MCZ). MALAYSIA: Perak Subur, April–July 1929, ♀ (Dalton, ZRC). INDONESIA: *Sumatra.* Si Rambé [Sirombu], sev. ♀ (Modigliani, NMW); Pedang, juv. (E. Reimoser, MCZ), ♀ (SMF); between Taroengen and Biruen, ♀♀♂ (MCZ); ? Afjeh [? Atjeh, ? Aljeh], April 1924, ♀ (S. A. R. Prince Léopold, IRSN); Harau Kloof, 24 April 1929, ♀ (S. A. R. Prince Léopold, IRSN); Fort de Kock [Bukittinggi], 900 m, 1924, 5♀ (E. Jacobsen, SMF); Bungar-Bondar (W. Sumatra), 14 April 1914, 3♀ (Schütz, SMF); Lumba Gaul [Pulau Lumba], 1500 m, 1 Sept. 1919 (O. Hagerup, ZMK). *Java.* Gebang, Bantar [? Bandjar], 1909, ♀ (Palmer and Bryant, MCZ); Pendjaloe, 31 Dec. 1928, 2♀ (S. A. R. Prince Léopold, IRSN); Buitenzorg [Bogor], 1906–1907, ♀ (T. Barbour, MCZ), Jan. 1922, ♀ (T. Mortensen, ZMK), 3♀ (NMW); Djakarta, 1957–1958, ♀ (D.M. Rees, AMNH). *Lombok Isl.* Center of island, ♀ (C. Auri-villius, NRS). *Borneo.* Pagata (Grabowski, ZMB); Moara Terveh [Muarateweh], 4♀ (Breitenstein, NMW). *Moluccas.* Celebes: Langoan Hot Springs, ♀ (MCZ); Tember Hot Springs, ♀ (MCZ); Tondano, ♀ (SMF). PHILIPPINES: *Luzon.* Manila, ♀ (W. M. Beck, AMNH); ♀ (ZMH), ♂ (MNHN); 1945, ♀ (W. R. Enns, AMNH); Alabong, 20 Jan. 1951, ♀ (J. Bergseng, FMC); Prov. Albay, ♀♂ (Jagor, ZMB); Baguio, Mtn. Prov., 3 Nov. 1945, ♀ (B. Malkin, AMNH); Umber, Cavite, 20 Dec. 1950, ♀ (J. Bergseng, FMC); Longayen, June–July 1945, ♂ (R. B. Burrows, AMNH). WEST NEW GUINEA [Djaya Pura]: Merauke, 1956, 1957, ♀ (Br. Monulph, RNHL). CAROLINE ISLANDS: *Yap.* Ruu Distr., 26 Aug. 1950, ♂ (R. J. Goss, BPBM); Colonia, July–Aug. 1950, ♂ (R. J. Goss, BPBM).

Argiope buehleri Schenkel

Figures 42–46; Map 2

Argiope bühleri Schenkel, 1944: 184, fig. 7, ♀. Female holotype from Soë, Timor, four female paratypes from Nitel-Tiki [? Nikiniki], Timor, in the Naturhistorisches Museum, Basel, examined.

Note. No others than the original specimens could be found in the collections available. It may be that these specimens belong to *A. reinwardti.*

Diagnosis. The rim of the epigynum is not as straight as that of *A. reinwardti*; the septum has an even, round curvature (Fig. 42) and is not flattened, as is that of *A. reinwardti.*

Argiope reinwardti (Doleschall)

Figures 47–55; Map 2

Epeira (*Argyropes*) *trifasciata* Doleschall, 1857: 416, pl. 1, fig. 3, ♀. One female holotype from Amboina [Ambon] in the Rijksmuseum van Natuurlijke Historie, Leiden, examined [not *A. trifasciata* (Forskål, 1775)].

Epeira reinwardti Doleschall, 1859: 31, pl. 1, fig. 3. Name given to illustrations of specimens from Java. Two syntypes, here labeled, the original specimens in the Rijksmuseum van Natuurlijke Historie, Leiden, examined.

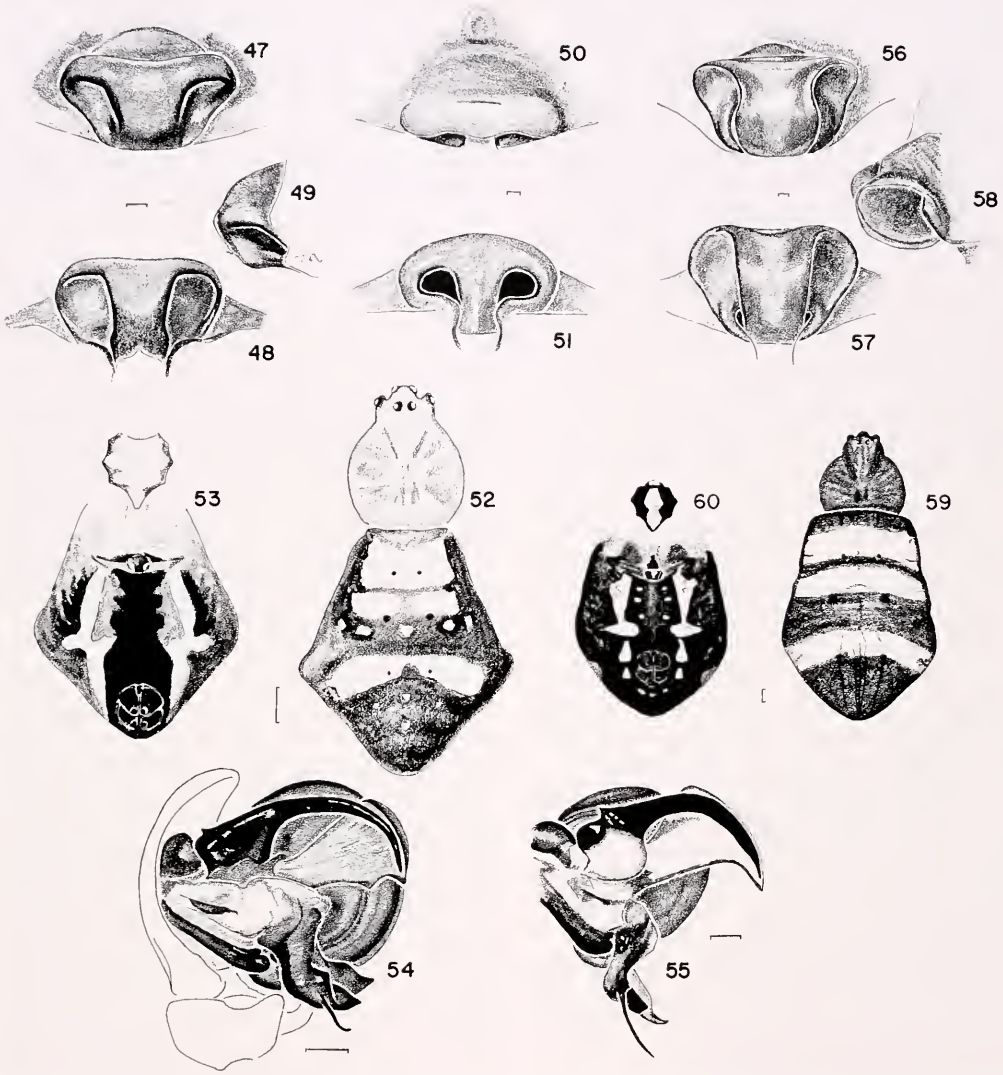
Argiope doleschalli Thorell, 1873: 520. New name for *Epeira trifasciata* Doleschall, preoccupied by *A. trifasciata* Forskål, 1775.

Argiope doleschalli sumatrana Hasselt, 1882: 18. Provisional new name for Sumatra specimens. Specimens lost in the Leiden museum.

Argiope concinna Thorell, 1881: 71. Female holotype from Aru Island [Arafura Sea] in the Museo Civico di Storia Naturale, Genova, examined. NEW SYNONYMY.

Argiope doleschalli bivittigera Strand, 1911b: 141. Last instar juvenile female holotype from Elat, Great Key [Kai Island, Banda Sea] in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

? *Argiope barbipoda* Strand, 1911: 144, pl. 5, fig. 44. Juvenile holotype from Grosz Key, Elat [Great Key,



Figures 47–55. *Argiope reinwardti* (Doleschall). 47–53. Female. 47. Epigynum, ventral. 48. Epigynum, posterior. 49. Epigynum, lateral. 50, 51. Penultimate instar, epigynal region. 50. Ventral. 51. Posterior. 52. Carapace and abdomen. 53. Sternum and abdomen. 54, 55. Left male palpus, mesal. 54 (Papua New Guinea). 55. (Western Sumatra).

Figures 56–60. *Argiope caesarea* Thorell, female. 56. Epigynum, ventral. 57. Epigynum, posterior. 58. Epigynum, lateral. 59. Carapace and abdomen. 60. Sternum and abdomen.

Scale lines. 0.1 mm, except Figures 52, 53, 59, 60, 1.0 mm.

Kai Island, Banda Sea] in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Argiope aetherea var. *confusa* Kulczynski, 1911: 475, fig. 47, ♀. One female syntype from Jenda [Jende], one female and one juvenile syntype from Manikion, New Guinea in the Polish Academy of Science, Warsaw, examined. NEW SYNONYMY.

Argiope aetherea var. *coniuncta* Kulczynski, 1911: 475, fig. 46, ♀. Female holotype from the region of upper Lake Jamur, New Guinea in the Polish

Academy of Science, Warsaw, examined. NEW SYNONYMY.

Argiope celebesiana Merian, 1911: 203, pl. 9, figs. 1–3. Female holotype from Celebes in the Naturhistorisches Museum, Basel, examined. NEW SYNONYMY.

Argiope reinwardti:—Roewer, 1942: 741. Bonnet, 1955: 693. Chrysanthus, 1971: 15, figs. 20–22, ♀, ♂. B. C. Robinson and M. H. Robinson, 1974: 145, pl. 3, ♀ (photo). M. H. Robinson, Lubin, and B. Robinson, 1974: 117–163. M. H. Robinson and B. Robinson, 1980: 10, 50, 54–60, 109, 191, figs. 22–24.

Notes. Argiope plana L. Koch from Australia, previously synonymized with *A. reinwardti*, is a synonym of *A. trifasciata*. *Argiope doleschalli bivittigera* Strand, although a last instar juvenile, has a weakly sclerotized epigynum and internal seminal receptacles (Figs. 50, 51). Other than the one from New Guinea, only one male was found in the collections available. This one from Sumatra, whose palpus has a shorter, thicker embolus (Fig. 55) and differently shaped median apophysis, indicates that specimens from Sumatra may belong to a different species. The females from Sumatra have a wider septum than the septum of the specimen from New Guinea illustrated (Figs. 47–49). Perhaps what is here considered one species consists of several; or, *A. caesarea* and *A. buehleri* may be subspecies of *A. reinwardti*.

The illustrations (Figs. 47–49, 52–53) were made from specimens from Mount Kaindi road, Wau, Papua New Guinea; Figure 55 from a male with an expanded palpus from West Sumatra.

Diagnosis. The dorsum of the pentagonal female abdomen has three transverse white bands on black (Fig. 52), similar to some specimens of *A. aetherea*. The epigynum distinguishes the two: in *A. reinwardti* it has an almost straight anterior rim, and the wide septum is dorsoventrally flattened; the posterior of the septum does not curve laterally into the depression (Figs. 47, 48). The palpus has a fan-shaped conductor, a simple clawlike embolus, and a median apophysis with a spur on the outside directed proximally (Fig. 54).

Variation. Specimens in the Berlin Museum have a different pattern, resembling that of *A. perforata*. Most are in poor condition, but they all came from the same area: coastal New Guinea between Madang and the Sepic River. Malaysian individuals have the sternum dark like the northern *A. caesarea*, and tubercles on the sides facing each coxa.

Natural History. Argiope reinwardti is found on the edge of forested slopes, sometimes rock faces, in the Wau area, Papua New Guinea. The web has a stabilimentum which is a cross, crossing the hub; but the stabilimentum is frequently absent or present only as one diagonal line (B. C. Robinson and M. H. Robinson, 1974; M. H. Robinson, Lubin, and B. Robinson, 1974). Courtship and mating behavior is reported in M. H. Robinson and B. Robinson, 1980. When the spider is disturbed while in the web, it will fall to the ground and instantaneously change the color of the abdomen; the light cells of the abdomen contract and the spider becomes earth colored. On the ground the spider lies still with its legs contracted (Bristowe, 1976).

Distribution. Malay Peninsula to New Guinea (Map 2).

Records. MALAYSIA: *Malay Peninsula.* Kuala Lumpur, Sept. 1921, ♀ (H. M. Pendlebury, ZRC); Tahan Riv., Pahang, 21 Nov. 1923, ♀ (H. M. Pendlebury, ZRC). INDONESIA: *Sabah.* Kabayau and Bundu Tuan, July 1925, ♀ (C. M. Enriquez, ZRC); Tanompek, 1500 m, July 1925, ♀ (C. M. Enriquez, ZRC). *Sumatra.* mountains above Pagaralam, 2♀ (MCZ); W Sumatra, 1974, ♀♂ (W. S. Bristowe, BMNH); Fort de Kock [Bukittinggi], 3♀ (Jacobson, NMW). *Java.* Djakarta, 1957–1958, ♀ (D. M. Rees, AMNH); Tjiboda [Ciboda], 28 Aug. 1922, ♀ (T. Mortensen, ZMK), April 1908, 2♀ (HCO); Tengger Mts., 1300 m, 16 June 1909, 3♀ (A. Berg, NRS); Buitenzorg [Bogor], 1904, ♀ (I. Jensen, ZMK); 4♀ (NMW), ♀♀ (Palmer and Bryant, MCZ). *Celebes.* Malino, ♀ (MCZ); Lokka on Pic of Bantaëng, 1150 m, ♀ (NMB); Pic of Bantaëng, 800–1000 m, ♀ (NMB). *Timor.* 2♀ (C. Auri-villius, NRS). *Moluccas.* Am-

boina [Ambon]: April 1908, ♀ (T. Barbour, MCZ); ♀ (Suykerbuyk, IRSN); ♀ (NMW). Ternate: 1906–1907, ♀ (T. Barbour, MCZ). CHRISTMAS ISLAND: numerous records (WAM, ZRC). NEW GUINEA: *West Irian* [Djaya Pura]. Hollandia [Djaya] (AMNH). *Papua New Guinea*. many records (AMNH, CNC, MCZ, BMNH, ZMB).

Argiope caesarea Thorell

Figures 56–60; Map 2

Argiope caesarea Thorell, 1897: 7. Two female specimens, probably not types, from Carin Cheba [Kareni], 1. Bia Pò, Burma in the Naturhistoriska Riksmuseet, Stockholm, examined. The types are recorded from Carin Birmaniae [Kareni] and Catun Cauri. Roewer, 1942, 1: 738. Bonnet, 1955: 683.

Argiope kalimpongensis Sinha, 1951: 77, fig. 3, ♀. Holotype from Kalimpong, Darjiling district, Bengal, India in the Zoological Survey of India, not available. NEW SYNONYMY.

Argiope sikkimensis Tikader, 1970, 64: 28, fig. 18, ♀. Female holotype from Rongli, East Sikkim, India in the Zool. Survey of India, not available. NEW SYNONYMY.

Note. It is uncertain if this is distinct from *A. reinwardti*; perhaps the male will clarify the status of *A. caesarea*. No differential characters were given to separate *A. reinwardti* or *A. caesarea* from *A. kalimpongensis* or *A. sikkimensis*, and I assume all belong to the same species.

Diagnosis. *Argiope caesarea* differs from *A. reinwardti* by the coloration of the sternum, being black on the sides (Fig. 60), and in that the rim of the epigynum narrows laterally (Figs. 56, 57).

Records. BURMA: Carin Hills [Kareni], 9000–10,000 m, 1885–1889, 3♀ paratypes of *A. caesarea* (L. Fea, ZMH). INDIA: Upper Assam, ♀ (Haberl, ZMB).

Argiope boesenbergi new species

Figures 61–66; Map 3

Argiope aetherea:—Karsch, 1878: 803. Bösenberg and Strand, 1906: 198, pl. 12, fig. 296, ♀. Yaginuma, 1960: 60, pl. 25, fig. 143, ♀. Misidentification, not *A. aetherea* (Walckenaer).

Coganargiope (*Mesargiope*) *aetherea*:—Kishida, 1936: 25.

Holotype. Female from Mt. Iwawaki, Osaka Pref., Japan, 20 Aug. 1954 (T. Yaginuma) in the collection of the Arachnological Society of East Asia in Ohtemon-Gakuin University, Osaka.

Notes. Since Karsch (1878) there are several species for which the name *A. aetherea* is used. Karsch gave the name *A. keyserlingi* to the species illustrated by Keyserling, 1865: 803, plate 19, figures 1, 2, ♀. But Keyserling specimens came from Wollongong, New South Wales, Australia; nor were they the same species as Walckenaer's *A. aetherea* from New Guinea. Bösenberg and Strand (1906), who had Japanese and northern Australian specimens, continued the confusion. *Argiope keyserlingi* has to be used for the species superficially similar to *A. aetherea* from southeastern Australia.

The illustrations of the female were made from a specimen from the Kiangsi Province, China; those of male from the mirror image of the right palpus of a Japanese paratype.

Diagnosis. The female has a diagnostic dorsal abdominal pattern (Fig. 64), yellowish silver and black in living specimens, somewhat similar to that of *A. picta*. Females differ from all other species by lacking the anterior bulge of the epigynum; in place of this structure the septum projects anteriorly into a keel with a median anterior groove (Figs. 61, 63), and the depressions on each side are not bordered anteriorly by a lip (Figs. 61–63). The palpus of the male has the embolus divided into two pieces (Fig. 66), unlike that of *A. amoena*: the distal piece is held by the conductor; both extend at a 90° angle to the axis of the palpus.

Distribution. Japan, China (Map 3).

Paratypes. JAPAN: Miyanoshita, [?*Miyagi Pref*. Miyato Shima] 1889, ♀ (B. Schmacker, SMF). *Osaka Pref*. 23 June 1946, ♀ (AMNH). *Nara Pref*. Kitayamakyo, 31 May 1951, ♂ (T. Yaginuma, MCZ); Yoshinoyama, Aug. 1980, ♀, 30 July 1981, ♀ (T. Yaginuma, ASEA); Yoshino, 14 July 1963, ♀ (T. Yaginuma, MCZ).

Records. JAPAN [?] Saga Kompira, ♀ (SMF). CHINA: *Chekiang Province*. Mokanshan, N. Gist Gee, Soochow, ♀ (MCZ).

Kiangsi Province. Hong San, 25 June 1936, ♀ (MCZ). *Fukien Province.* Changchow, ♀ (AMNH).

Argiope amoena L. Koch

Figures 67–72; Map 3

Argiope amoena L. Koch, 1878: 735, pl. 15, fig. 1, ♀. Female holotype from Japan in the British Museum, Natural History, examined. Bösenberg and Strand, 1906: 199, pl. 4, fig. 19, pl. 12, fig. 290, ♀, ♂. Strand, 1918: 95, pl. 2, fig. 37, ♀. Roewer, 1942: 740. Bonnet, 1955: 672. Yaginuma, 1960: 60, pl. 25, fig. 142, ♀. Song, 1980: 99, fig. 44, ♀.

Coganargiope amoena:—Kishida, 1936: 18.

Argiope davidi Schenkel, 1963: 137, fig. 80, ♂. Male holotype without palpi from Kiangsi in the Muséum National d'Histoire Naturelle, Paris, examined. NEW SYNONYMY.

Notes. The holotype of *A. davidi* has lost its palpi. Schenkel's illustration, however, indicates that it is a male of *A. amoena.*

The embolus with duct tears off when mating. In one female two emboli were found on the same side, one completely inserted (as illustrated) in the epigynum, and another with only the tip wedged in. The specimens illustrated came from southeastern Kiangsi Province, China.

Diagnosis. This species is close to *A. magnifica* and *A. boesenbergi.* The female differs by the contrastingly banded abdomen (Fig. 70), and by the epigynum which is longer than wide, with a U-shaped rim and sclerotized anterior bulge (Fig. 67), with the short septum widening into a very long posterior plate (Figs. 68, 69). The palpus differs by the much longer embolus flaring proximally (Fig. 72).

Distribution. Japan, China (Map 3).

Records. JAPAN: *Kyoto Pref.* Kyoto, 18 July 1980, ♀ (T. Yaginuma). *Okayama Pref.* Okayama, 10 July 1976, ♂ (Nishikawa, ASEA). *Osaka Pref.* Nishinomiya, June 1946, ♀♀ (W. Spector, AMNH). *Saitama Pref.* Tokyo, May 1931, ♀ (MCZ). [?] Kogoshima [Gogo-Shima Isl.]. [?] Kyashu, June 1958, ♀ (N. L. H. Krauss, AMNH). *Nara Pref.* Mt. Katsuragi, 13 Aug. 1951, ♀ (H. Yoneda, AMNH). *Gifu Pref.* 25 Aug. 1951, ♀ (T. Yaginuma). *Kanagawa Pref.* Misaki, July 1917, ♀ (T. Mortensen, ZMK); Yokohama, 1889, 4♀ (G. Schmacker, B. Schmacker, SMF). KOREA: Sangju, 21 Aug. 1956, ♀ (K. Paik, AMNH). CHINA: (Song, 1980). *Kiangsi Prov.* Soochow (AMNH); Hong San, June–July 1936, ♀♀♂♂ (L. Gressitt, MCZ). *Chekiang Prov.* Mokanshan [Mo-kan Shan], N. Gist Gee of Soochow, 1936, ♀♀ (L. Gressitt, MCZ); Shanghai, June 1906, ♀♀ (S. C. Thompson, CAS). *Fukien Prov.* Kuliang near Foochow [Fuchou], 750 m, July 1926, ♀♀ (C. R. Kellogg, CAS). *Hupeh Prov.* Suisapa, Lichuan Distr., 22 July 1943, ♀ (L. Gressitt, CAS), 19 Aug. 1948, ♀ (CAS). *Szechuen Prov.* Dec. 1914, ♀ (BMNH).

Argiope magnifica L. Koch

Figures 73–80; Map 3

Argiope magnifica L. Koch, 1871: 27, pl. 2, fig. 6, ♀. One female from Bowen, Queensland, and one badly damaged female from Queensland in the Godeffroy collection of the Zoologisches Museum, Universität Hamburg, examined.

Argiope aemula:—Chrysanthus, 1971: 9, figs. 1–3, ♂. M. H. Robinson and B. Robinson, 1973: 59; B. Robinson and M. H. Robinson, 1974: 145–159, pl. 1, ♀

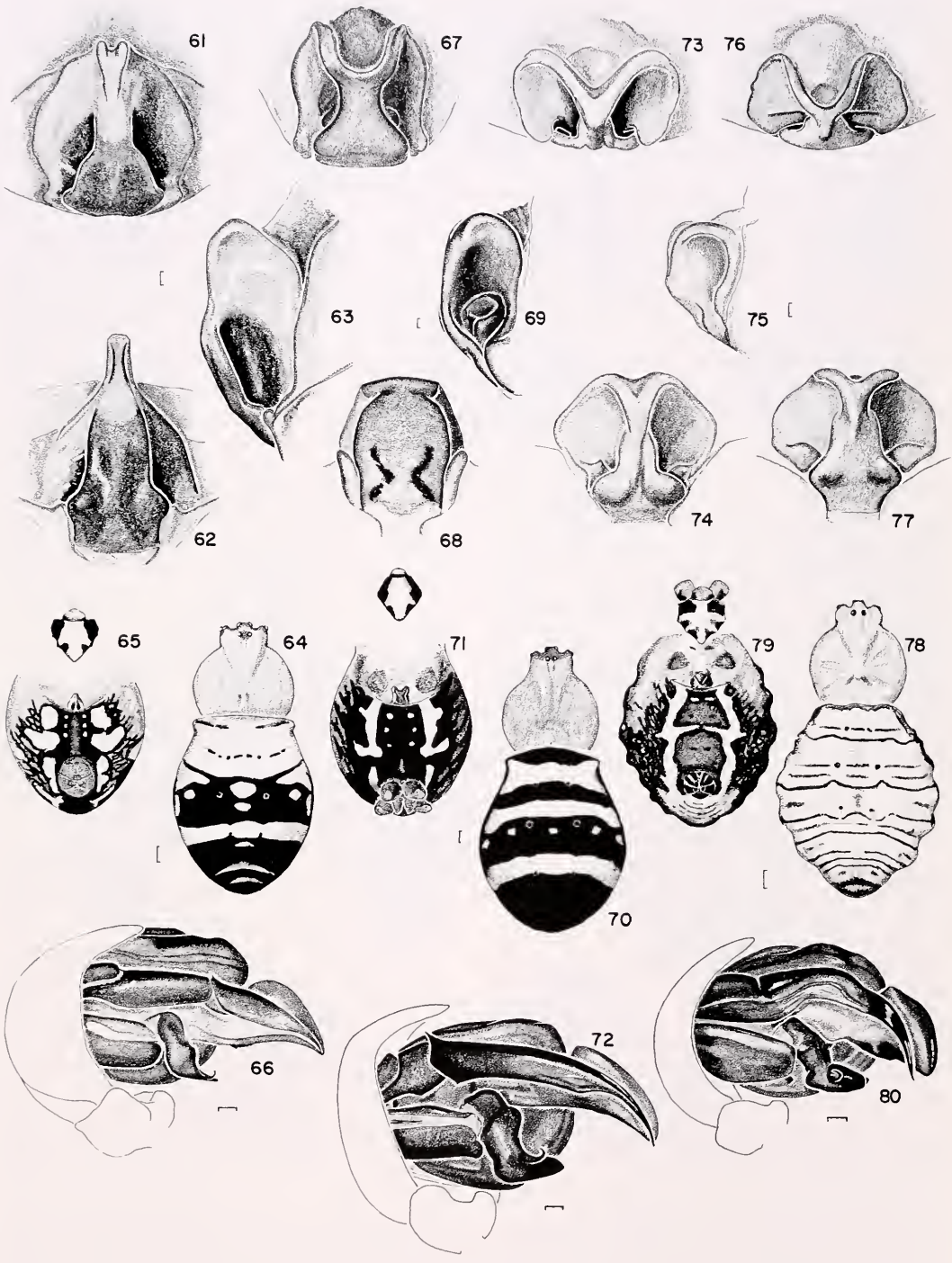
→

Figures 61–66. *Argiope boesenbergi* n. sp. 61–65. Female. 61. Epigynum, ventral. 62. Epigynum, posterior. 63. Epigynum, lateral. 64. Carapace and abdomen. 65. Sternum and abdomen. 66. Left male palpus, mesal.

Figures 67–72. *Argiope amoena* L. Koch. 67–71. Female. 67. Epigynum, ventral. 68. Epigynum, posterior. 69. Epigynum, lateral. 70. Carapace and abdomen. 71. Sternum and abdomen. 72. Left male palpus, mesal.

Figures 73–80. *Argiope magnifica* L. Koch. 73–79. Female. 73, 76. Epigynum, ventral. 74, 77. Epigynum, posterior. 75. Epigynum, lateral. 73–75. (Cairns, Queensland). 76, 77. (Wau, Papua New Guinea). 78. Carapace and abdomen. 79. Sternum and abdomen. 80. Left male palpus, mesal.

Scale lines. 0.1 mm, except Figures 64, 65, 70, 71, 78, 79, 1.0 mm.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(photo). M. H. Robinson, Lubin, and B. Robinson, 1974: 117–163. M. H. Robinson and B. Robinson, 1980: 10, 21–22, 43–58, 60, 70, 73, 82–83, 85, 89, 111, 190–192, 207, figs. 19–21, ♀♂ (photo) [misidentification, not *A. aemula* (Walckenaer)].

Notes. The specimens of *A. magnifica* from Bowen may not be the types, since the type of *A. magnifica* came from Port Mackay and Rockhampton.

The name *A. magnifica* had previously been erroneously synonymized with *A. aemula* (Roewer, 1942: 739).

Some females have fine tubes hanging out of the opening in the epigynum depression, the duct of a male embolus.

Figures 73–75 came from a specimen from Cairns, Australia; Figures 76–80 from Wau, Papua New Guinea.

Diagnosis. Females can be separated from most other *Argiope* by the uniform dorsal color of the abdomen, with fine black transverse lines (Fig. 78). Unlike the similar *aemula*, the posterior plate of the epigynum bends anteriorly and meets the scape on the venter (Figs. 73, 76); the septum continues below as a ridge in the middle of the posterior plate (Figs. 74, 77). The anterior bulge has a characteristic shallow circular posterior depression between the angle of the rim (Figs. 73, 76). The lateral edges of the depression appear unfinished and flat, unlike those of *A. aemula*.

The palpus has a long, gently curved embolus, and the median apophysis has its spur on its mesal face (Fig. 80).

Natural History. In the Wau area, Papua New Guinea this species is found in open grassy locations (B. C. Robinson and M. H. Robinson, 1974). The web usually has an X-shaped stabilimentum whose branches do not cross the hub region. The attack behavior is described in B. C. Robinson and M. H. Robinson, 1974; courtship and mating behavior in M. H. Robinson and B. Robinson, 1980.

Distribution. New Guinea, New Britain, Solomon Islands, Queensland (Map 3).

Records. PAPUA NEW GUINEA: *Eastern Highlands.* Arau, Oct. 1959, (J. Gunn, AMNH). *Morobe Distr.* Finschhafen, ♀ (NMW); Herzog Mts., Vagau, 1220 m, 17 Jan. 1965, 2♀ (M. E. Bacchus, BMNH). Mt. Kaindi, nr. Wau, May 1959, ♀♀ (Archbold Exped., AMNH); Wau, 18 March 1979, ♀♀♂ (several coll., MCZ); Kabwum [?], Huon Peninsula, Nov. 1964, ♀ (H. M. van Deusen, AMNH); Gemcheng, Huon Penins., 11–12 April 1955, ♀ (E. O. Wilson, MCZ). *Madang Distr.* Finistere Mts., Naho River Valley, Budemu, 1270 m, 25 Oct. 1964, ♀ (M. E. Bacchus, BMNH); Kundiawa near Gumine, 10 Aug. 1972, ♀ (CNC). NEW BRITAIN: 2♀ (Tring Mus., BMNH); ♀ (Finsch, ZMB); Ralum [near Rabaul], 17 May 1896, ♀ (F. Dahl, ZMB); Simpsonhafen [Rabaul], May 1909 (Schwede, ZMB). SOLOMON ISLANDS: Guadalcanal (many records); Marova Lake, ♀ (W. M. Mann, MCZ). AUSTRALIA: *Queensland.* Cairns, Aug.–Sept. 1938, ♀ (R. G. Wind, MCZ); 88 km SW Mt. Garnet, 650 m, 5 Nov. 1962, ♀ (E. S. Ross, CAS); Bellenden Ker, May, ♀ (E. Mjöberg, NRS); Bowen, 1882, ♀ (NMW).

Argiope bruennichi (Scopoli)

Figures 81–86; Map 3

Aranea bruennichi, Scopoli, 1772: 125. Original specimen from Carniolia [Carinthia].

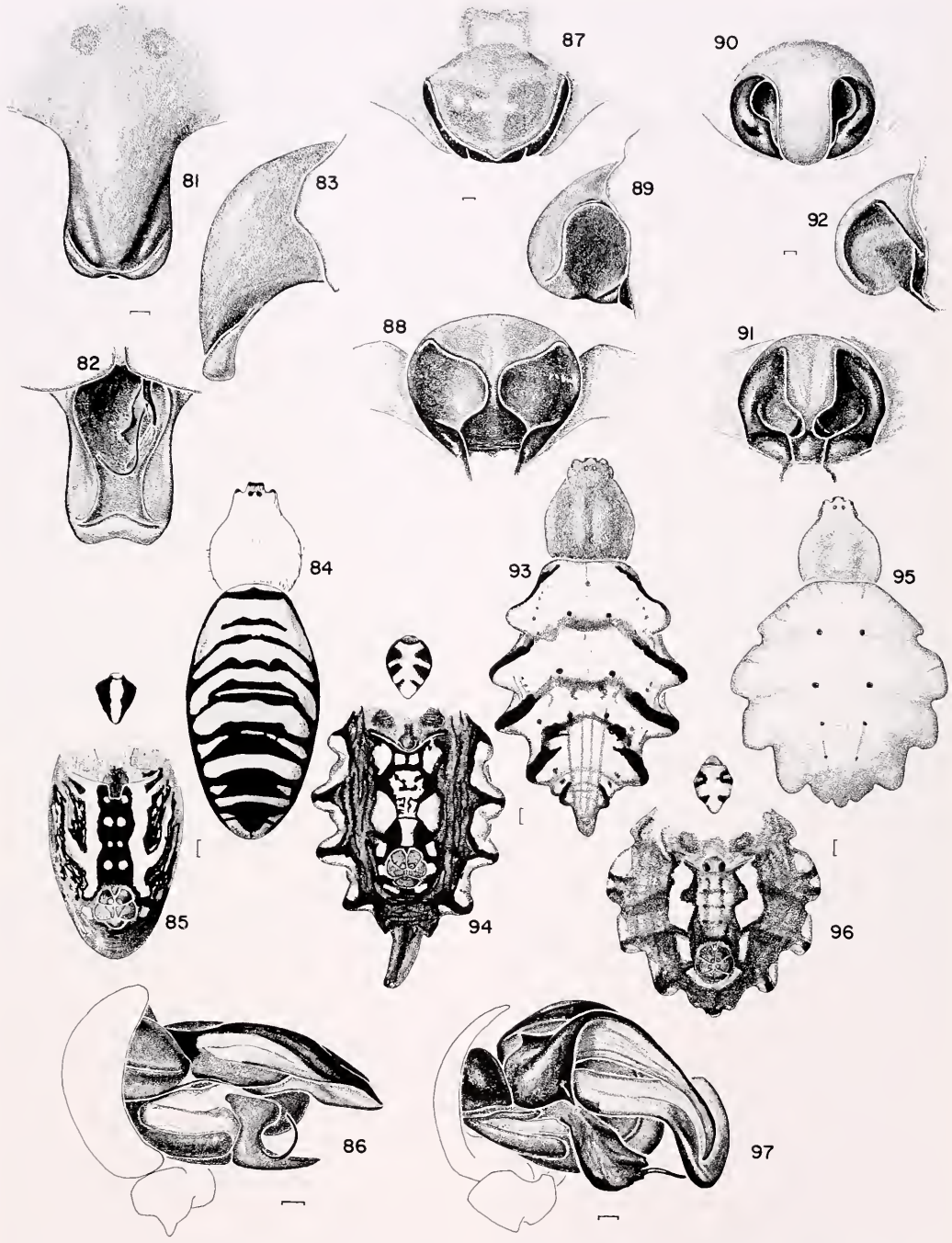
Argiope bruennichi:—Thorell, 1873: 518. Wiehle, 1931: 14, figs. 4b, 5a, 11–17. 1♀♂ Roewer, 1942: 734. Bonnet, 1955: 678. Yaginuma, 1960: 60, pl. 25, fig. 144, ♀. Song, 1980: 97, fig. 43, ♀.

Argiope bruennichi orientalis Strand, 1907a: 416. Female holotype from Java [? erroneous locality] deposited in the Zool. Institute of the University of Tübingen, examined. Now deposited in the Senckenberg Museum. NEW SYNONYMY.

Miranda zabonica Chamberlin, 1924: 17, pl. 4, fig. 34. Male holotype from Soochow [? Hsüchou, Kiangsi Prov.], China in the National Museum of Natural History, Washington, D.C., examined. NEW SYNONYMY.

Note. According to Strand, *A. bruennichi orientalis* is larger than the European specimens but has a similar, very distinct epigynum. The female here illustrated came from China, the male from Japan.

Diagnosis. The genitalia are most similar to those of *A. aurantia* of North America (Levi, 1968: 56). As in *A. aurantia*, the epigynum is a wide scape with a median dorsal hollow, lacking a septum



Figures 81–86. *Argiope bruennichi* (Scopoli). 81–85. Female. 81. Epigynum, ventral. 82. Epigynum, dorsal. 83. Epigynum, lateral. 84. Carapace and abdomen. 85. Sternum and abdomen. 86. Left male palpus, mesal.

Figures 87–97. *Argiope lobata* (Pallas). 87–96. Female. 87, 90. Epigynum, ventral. 88, 91. Epigynum, posterior. 89, 92. Epigynum, lateral. 93, 95. Carapace and abdomen. 94, 96. Sternum and abdomen. 87–89, 93, 94. (Burma). 90–91, 95, 96. (Java). 97. Left male palpus, mesal.

Scale lines. 0.1 mm, except Figures 84, 85, 93–96, 1.0 mm.

(Fig. 82). However, the dorsal abdominal markings differ from the American *A. aurantia* (Fig. 84).

The male palpus has a long, almost straight embolus, its tip held by a conductor; the median apophysis has a long, curved filamentous spur (Fig. 86) and, like *A. aurantia*, a row of irregular large teeth laterally (not visible in Fig. 86). The stipes (base of embolus), unlike *A. aurantia* or any other species, has a soft, transverse slit (Fig. 86).

Distribution. Eurasia to Japan and China, perhaps Australia (Map 3).

Records. JAPAN: *Kanagawa Pref.* Yokohama, 1889, ♀ (Schmacker, SMF.) *Wakayama Pref.* Shiono Misaki, 29 Oct. 1973, ♀ (W. C. Sedgwick, SC). 23 Oct. 1951, ♀ (T. Yaginuma, AMNH); Shirahama, 29 Oct. 1972, ♀ (W. C. Sedgwick, SC). Negorosan, Naga-gun, 19 Aug. 1950, ♂ (H. Yoneda, MCZ); Mt. Katsuragi, Naga-gun, 13 Aug. 1951, ♀ (S. Kobayashi, AMNH); Yoshino, 6 Aug. 1980, ♀; 22 Aug. 1981, ♂ (T. Yaginuma, MCZ). *Kyoto Pref.* Kyoto, ♀ (W. C. Sedgwick, SC). KOREA: Sach'ang-ni [Sojong-ni], 16 Aug. 1953, ♀ (T. J. Cohen, AMNH); Yach'on-ni, Su-chon River, 18 Aug. 1953, ♀ (AMNH); Taegu, 28 July 1955, ♀ (K. Paik, AMNH); 24 km. SSE Kumwha, Sept. 1953, ♀ (T. J. Cohen, AMNH); Aug. 1953, ♂ (T. J. Cohen, AMNH). CHINA: (Song, 1980). *Hupeh Prov.* Suisapa, 22 Aug. 1948, ♀ (Djou, CAS). *Chekiang Prov.* Mokanshan [Mo-Kan Shan mountain], Soochow [Suchou]. AUSTRALIA: *New South Wales.* Sydney [locality error ?], ♀ (AMS).

Argiope lobata (Pallas)

Figures 87–97; Map 3

Aranea lobata Pallas, 1772: 46, pl. 3, figs 14, 15. Specimens from unknown locality [presumably from the Ukraine], lost.

Argiope arcuata Simon, 1884: 343. Female holotype from near Minula, Irriwaddy River, Burma in the Muséum National d'Histoire Naturelle, Paris, examined. Pocock, 1900: 220, fig. 70, ♀. Roewer, 1942: 787. Bonnet, 1955: 673. NEW SYNONYMY.

Argiope lobata:—Roewer, 1942: 735. Bonnet, 1955: 687. Levi, 1968: 336, figs. 25–38, ♀♂.

Note. The illustrations for Figures 87–89, 93, 94 were made from the holotype of *A. arcuata*; Figures 90–92, 95, 96 from a specimen from Java; Figure 97 from a male from Corsica.

Diagnosis. The dorsally silvery abdomen with large lobes all around (Figs. 93, 95) is diagnostic. The epigynum is quite variable, lacking a distinct rim, and the anterior bulge continues as a more or less wide lobe which posteriorly constricts into a narrow median septum (Figs. 88, 91) (see also Levi, 1968: figs. 25–35). On each side of the base of the male's embolus is a recurved thorn (Fig. 97).

Distribution. This species is found from the Mediterranean to China (Roewer, 1942), Burma to New Caledonia and northern Australia (Map 3).

Records. INDIA: Bombay, ♀ (HCO); Nilgiri Hills, Dekan [Madras] (SMF). BURMA: 15 Oct. 1922, ♀ (B. Brown, AMNH). INDONESIA: *Java.* ♀ (coll. by Natur. Hist. Comm., early in the 19th cent., RNHL). AUSTRALIA: *Queensland.* "northern," ♀, No. KS 6182 (AMS). NEW CALEDONIA: ♀ (E. Simon, BMNH).

Argiope protensa L. Koch

Figures 98–106; Map 3

Argiope protensa L. Koch, 1872: 211, pl. 18, fig. 8, ♀. Female holotype from Bowen [Port Denisson, Queensland] in the Godeffroy collection, Zoologisches Museum, Universität Hamburg, examined. Roewer, 1942: 743. Bonnet, 1955: 693. Chrysanthus, 1971: 15, figs. 15–19, ♀.

Argiope syrmatica L. Koch, 1872: 213, pl. 18, fig. 9, ♀. Female holotype from Bowen [Port Denisson], Queensland in the Museum of the University of Hamburg, examined.

Epeira attenuata Urquhart, 1884: 33, pl. 9, fig. 1, ♀. Female holotype from New Zealand, lost.

Arachnura longicauda Urquhart, 1884: 34, pl. 9, fig. 2, ♀. Female holotype from New Zealand, lost.

Argiope multifasciata Thorell, 1892: 226. Juvenile holotype from Singapore [? locality error] in the National Museum of Ireland, Dublin, examined. NEW SYNONYMY.

Argiope extensa Rainbow, 1897: 22(3): 519, pl. 17, fig. 5, ♀. Female holotype from Guildford [? New South Wales], Australia, KS 6413 in the Australian

Museum, Sydney, examined. Roewer, 1942: 742. Bonnet, 1955: 685. Mascord, 1970, pl. 34, fig. 134, ♀ (photograph).

Argiope pallida Rainbow, 1897: 521, pl. 17, fig. 6, ♀. Female holotype from Queanbeyan, New South Wales, KS 7111 in the Australian Museum, Sydney, examined. NEW SYNONYMY.

Argiope gracilis Rainbow, 1897: 522, pl. 17, fig. 7, ♀. Female specimen from Queanbeyan, Australian Museum, Sydney, examined. Holotype allegedly from Bungendore (not *A. gracilis* Blackwall). NEW SYNONYMY.

Argiope haynesi Hogg, 1914: 73, pl. 1, fig. 3, ♀. Female syntypes from Monte Bello Islands, Western Australia, in the British Museum, Natural History, examined. NEW SYNONYMY.

Argiope gracillima Roewer, 1942: 742. New name for *A. gracilis* Rainbow, preoccupied.

Notes. Thorell's *A. multifasciata* is almost certainly this species. Thorell noticed the similarity but named it because it came from Singapore. Was it introduced to Singapore? Is there a similar uncommon native species, or is the locality in error?

A female marked *A. gracilis* by Rainbow, but from Queanbeyan, is apparently the type of *A. gracilis* since it is the specimen which Rainbow illustrated: the shape of the abdomen and the pigment distribution in the illustration and specimen examined are alike.

The female was illustrated from a specimen from New Zealand (Figs. 98–103). The male was illustrated (Fig. 106) from an individual from Swan River, Australia (MCZ). Figure 105 was prepared from the holotype of *A. pallida*; Figure 104 from a female from Fitzroy Island, northern Queensland.

Diagnosis. Argiope protensa, unlike other species except *A. probata*, has a narrow abdomen overhanging and extending beyond the spinnerets (Figs. 102–105). Unlike the epigynum of *A. probata*, the openings face dorsally toward the venter of abdomen (Figs. 98–101).

The male can be told by the long curved embolus, whose tip is held by a conductor that is directed proximally. Unlike other species, the median apophysis points proximally and has a long S-shaped spur in the same direction (Fig. 106).

Variation. The shape of the abdomen is very variable: short, with almost no tail (Fig. 105), or a post-spinneret tail of variable length (Figs. 103, 104). The sternum of many specimens has pairs of tubercles facing the coxae. At present I believe they are all one species because of the similarity of the genitalia. The size range of females is 13 to 21 mm. Mascord (1970, Australian Spiders in Colour) presented photographs under the name of *A. protensa* (fig. 130), *A. extensa* (fig. 134), and *A. syrmatica* (fig. 135).

Distribution. Australia, New Zealand (Map 3).

Records. AUSTRALIA: *Queensland.* Townsville, March 1927, ♀ (G. Dennes, AMS); Mt. Isa, 1980, ♀ (AMS); Hughenden, ♀ (AMS); Alice Riv., ♀ (E. Mjöberg, NRS). *New South Wales.* Mascot, 13 March 1968, ♀ (R. Mascord, AMS); Richmond North, 1 March 1972, ♀ (R. McDonald, AMS); Springwood, 27 Dec. 1966, ♀ (A. E. Speechley, AMS); Queanbeyan, ♀ (AMS); Colo Vale, ♀ (AMS); The Rocks, Sydney, 19 March 1967, ♀ (AMS); Maylands, 4 May 1938, ♀ (C. L. Henley, WAM); Wyangarie, ♀ (AMS); Scone, ♀ (AMS); Mittagong, 7 Nov. 1974 (B. Collins, AMS). *Victoria.* Gisborne, ♀ (AMS). *A.C.T.* Glaninderra, Canberra, apple orchard, 14 Feb. 1964, ♀ (CNC). *Northern Territory.* Alice Springs, shrubs, ♂ (J. Wunderlich, WC); 18 km N Alice Springs, 625 m, 28 Oct. 1962, ♀ (E. S. Ross, CAS); Macdonald Downs, 400 m, 30 Oct. 1962, ♀♂ (E. S. Ross, CAS); Kulgera, ♀♀ (B. Greenwood, WAM). *Western Australia.* Geraldton; 27 km N Payne's Find, 400 m; 10 km N Mandurah; Mt. Magnet, 410 m; Milly Milly; Rossmore, ♀; Sir Graham Moore Isl. nr. Anjo Penins.; Kimberley Distr.; St. George Range; Montebello Isls.; Milling, lowland flats; Kathleen Valley, wasp nest; Kalgoorlie; Newmarracarra; Wembley; Tombrey; Bedford Park; Joondana; Calbarri; Gee Gie Outcamp; Murchison; Perth; Midland Junction; Morley; Florest Park; Carrolligooda Well; Brown Bone Cave, Pinnacles Desert; City Beach,

nr. Riffle Range; Youanmi; Doodlakine; Prairie Downs. *South Australia*. Kangaroo Isl., 7 km W of Emu Bay, 6 Dec. 1977, ♀ (D. C. F. Rentz and B. G. F. Rentz, CSIRO).

Argiope probata Rainbow

Figures 107–111; Map 3

Argiope probata Rainbow, 1916: 91, pl. 21, fig. 13, ♀. Female and one juvenile male syntypes from Pentland, Queensland, Australia, KS 6157 in the Australian Museum, Sydney, examined. Roewer, 1942: 743. Bonnet, 1955: 693.

Argiope ocyaloides:—Mascord, 1978: 6 (photograph) [misidentification].

Note. The illustrations of the female (Figs. 107–110) were prepared from the type specimen. The male's first femur has long macrosetae, six on the right, five on the left, standing up and each more than three femur diameters' length. There are smaller macrosetae on all tibiae and proximal parts of metatarsi. The male (Fig. 111) is from Wolfram, Queensland, and has not been collected with the female.

Diagnosis. The female differs from *A. protensa* by the flat epigynum facing ventrally (Fig. 107); the male by the embolus having the tip doubled up over its base (Fig. 111). The median apophysis has an enormous distal projection (Fig. 111).

Variation. Some specimens have a longer tail, others a much shorter one than pictured in Figures 109 and 110.

Records. AUSTRALIA: *Queensland*. Wolfram, 11 Feb. 1972, ♂ (N. C. Coleman, AMS); 8 Aug. 1971, ♀ (R. E. Mascord, AMS); Mareeba, 8 Feb. 1970, ♀♂ (N. C. Coleman, AMS).

Argiope trifasciata (Forskål)

Figures 112–119; Map 3

Aranea trifasciata Forskål, 1775: 86. Original specimens from Cairo [Egypt], lost.

Argiope avara Thorell, 1859: 299. Female syntypes from San Francisco, California and Oahu, Honolulu, in the Naturhistoriska Riksmuseet, Stockholm, examined. Chrysanthus, 1971: 12, figs. 9–12.

Argiope plana L. Koch, 1867: 181. Four female syntypes from Peak Downs [southern Queensland] and one from Bowen, Queensland in the Godeffroy collection of the Zoologisches Museum, Universität Hamburg, examined. NEW SYNONYMY.

Argiope fasciata:—Keyserling, 1886: 133.

Argiope avara kauaiensis Simon, 1900: 477. One female syntype from Kauai Island, Hawaii in the Bishop Museum, Honolulu, not examined.

Metargiope trifasciata:—F. P.-Cambridge, 1903: 451, pl. 43, figs. 2, 3, ♀, ♂. Kishida, 1936: 17.

Austrargiope plana:—Kishida, 1936: 17.

Argiope trifasciata:—Roewer, 1942: 733. Bonnet, 1955: 694. Levi, 1968: 340, pl. 1, figs. 58–72, 74–91, ♀, ♂. M. H. Robinson, Lubin, and B. Robinson, 1974: 128.

Brachygea platycephala di Caporiacco, 1947: 24. Male holotype from British Guyana in the Zoological Museum of the University of Florence, examined. NEW SYNONYMY.

Argiope pradhani Sinha, 1951: 76, fig. 2, ♀. Female holotype from Saran, Bihar, India in the Zoological Survey of India, not available. NEW SYNONYMY.

Notes. The name of *A. plana* had previously been considered a synonym of *A. reinwardti* (Doleschall). Sinha's illustrations of *A. pradhani* appear to be those of *A. trifasciata*.

The illustrations (Figs. 112, 117, 119) were made from Hawaiian specimens; Figure 118 from a specimen from New Caledonia.

Diagnosis. The dorsum of the abdomen is oval and has transverse black lines (Figs. 115, 118). The two ventral paraxial lines

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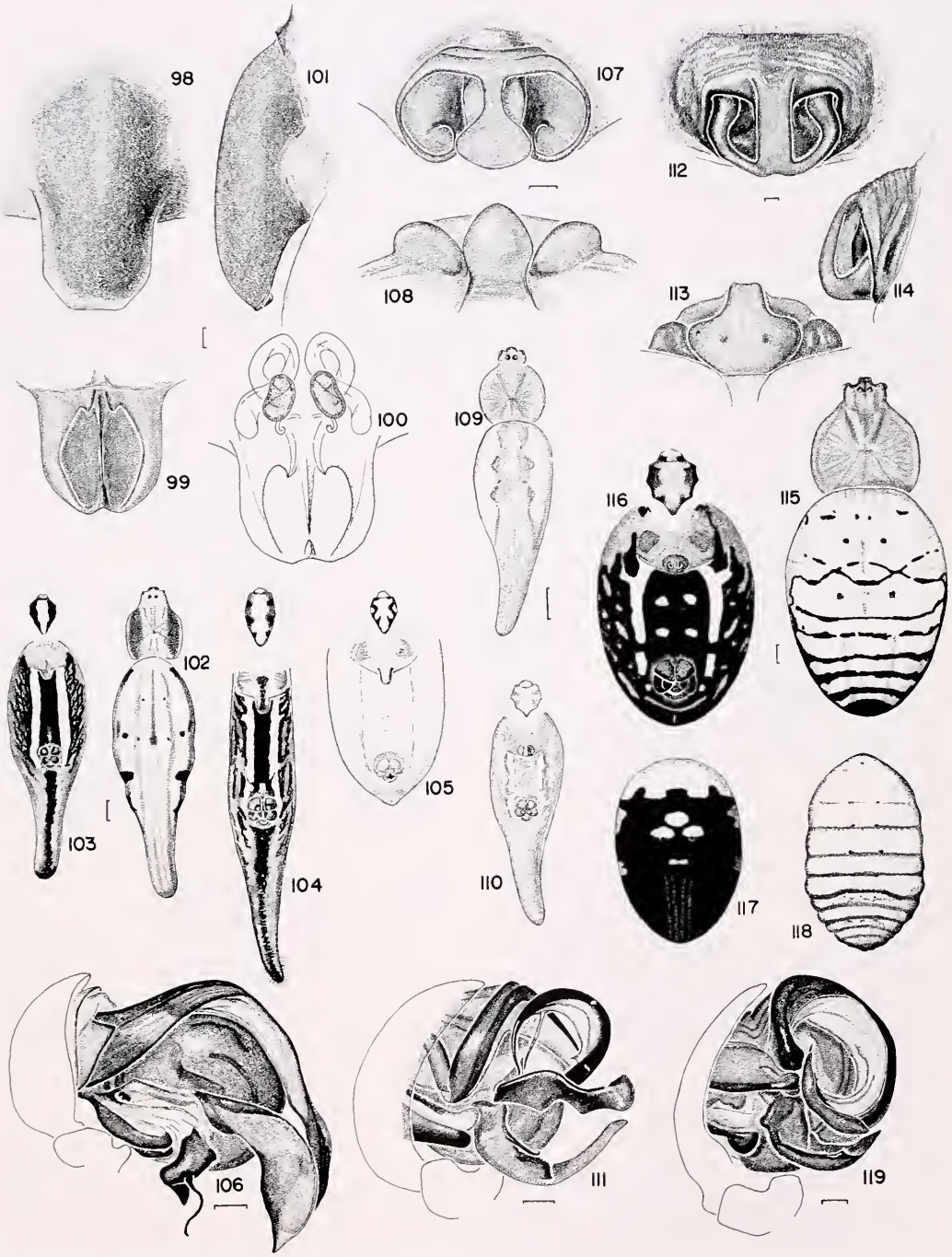
Figures 98–106. *Argiope protensa* L. Koch. 98–105. Female. 98. Epigynum, ventral. 99. Epigynum, dorsal. 100. Epigynum, dorsal, cleared. 101. Epigynum, lateral. 102. Carapace and abdomen. 103–105. Sternum and abdomen. 103. (New Zealand). 104. (Northern Queensland). 105. (New South Wales). 106. Left male palpus, mesal.

Figures 107–111. *Argiope probata* Rainbow. 107–110. Female. 107. Epigynum, ventral. 108. Epigynum, posterior. 109. Carapace and abdomen. 110. Sternum and abdomen. 111. Left male palpus, mesal.

Figures 112–119. *Argiope trifasciata* (Forskål). 112–118. Female. 112. Epigynum, ventral. 113. Epigynum, posterior. 114. Epig-



ynum, lateral. 115. Carapace and abdomen. 116. Sternum and abdomen. 117, 118. Abdomen, dorsal. 115, 116. (Oahu, Hawaii). 117. (Kauai, Hawaii). 118. (New Caledonia). 119. Left male palpus, mesal.

Scale lines. 0.1 mm, except Figures 102–105, 109, 110, 115–118, 1.0 mm.

include a black area containing a variable number of pairs of white patches (Fig. 116). Unlike females of other species, the anterior bulge of the epigynum lacks the distinct rims which fuse into the septum, and instead the septum anteriorly overhangs the rim (Fig. 112). Posterodorsally, the septum widens into a bottle-shaped posterior plate (Fig. 113). Within the depression the posterior plate is wide and hollowed out on each side (Fig. 112).

Unlike that of other species of the region, the conductor and embolus coil and face ventrally (Fig. 119); the median apophysis has only a minute filamentous spur on its edge.

Variation. The dorsum of the abdomen of specimens from Kauai Island, Hawaii is black with a light anterior (Fig. 117), resembling *Argiope bougainvilla* from the Solomon Islands and *Cyrtophora moluccensis* (Doleschall). Simon considered this coloration a subspecies. Females from Australia and New Caledonia have the sides of the abdomen slightly scalloped (Fig. 118).

Natural History. Argiope trifasciata occurs on roadsides and in grasslands in the Wau Valley, Papua New Guinea (M. H. Robinson, Lubin, and B. C. Robinson, 1974).

Distribution. Probably worldwide in the temperate and tropical areas. Absent from Europe and Japan. Very common in Hawaii (Map 3).

Records. HAWAIIAN ISLANDS: "Sandwich Island," ca. 1864, ♀♀ (A. Garett, MCZ). *Oahu.* 28 March 1889, ♀♀ (Galathea Exped., ZMK); Koko Head; Mt. Tantalus, Waimano Ridge; Honolulu; Kauloa Point; Manoa Valley, Mokuleia; Waialua; Kailua; Wahiarra. *Kauai.* Alakai Swamp; Wailua; Kilaua; Kau Distr., volcano road. *Hawaii.* Kamulea; Lanai (?); Mauna Loa Truck Trail. NEW GUINEA: Port Moresby; McLong Island (?). BISMARCK ARCHIPELAGO: South Hermit Isl., 15 Feb. 1952, ♀ (T. C. Campbell, CSIRO). AUSTRALIA: *Queensland.* Eidsvold; Gordonvale; Bluff Down; Maylands; Bicton. *New South Wales.* Mittagong; Long Bay; Yerrinbool; Kurnell; Malabar; Sydney; Kingscliff; Jenolan State Forest; Bilpin. *Australian Capitol Territory.* Canberra, 6 April 1979, ♀, 5 March 1935 (A. L. Tonnor, CSIRO). *Victoria.* Brunswick, 20 May 1966, ♀ (E. George, WAM). *Northern Territory.* Charters Towers; Mt. Molloy. *Western Australia.* Fitzgerald River; Greenshields; Marmion; Bridgetown; Kings Park; Leederville; Maylands; Rossmorine; Subiaco; Gosnells; East Fremantle; Perth; Hellfire Bay Camp, swamp; Freemantle; Applecross. NEW CALEDONIA: Quatom Valley; Nouméa; N of Tomo. SRI LANKA: "Ceylon," 6♂ (HCO). INDONESIA: *Sumatra.* Balinghe [Balinge], ♀♀ (Modigliani, NMW).

Argiope bullocki Rainbow

Figures 120–123; Map 4

Argiope bullocki Rainbow, 1908: 46, fig. 3, ♀. Female holotype from Parkville, near Scone, New South Wales, #KS 2464 in the Australian Museum, Sydney, examined. Roewer, 1942: 741. Bonnet, 1955: 683.

Diagnosis. Argiope bullocki differs from *A. probata* by having a shield-shaped abdomen (Fig. 122), and from *A. ocyaloides* and *A. doboensis* by having the rim of the epigynum laterally completely surround the circular depressions (Fig. 120).

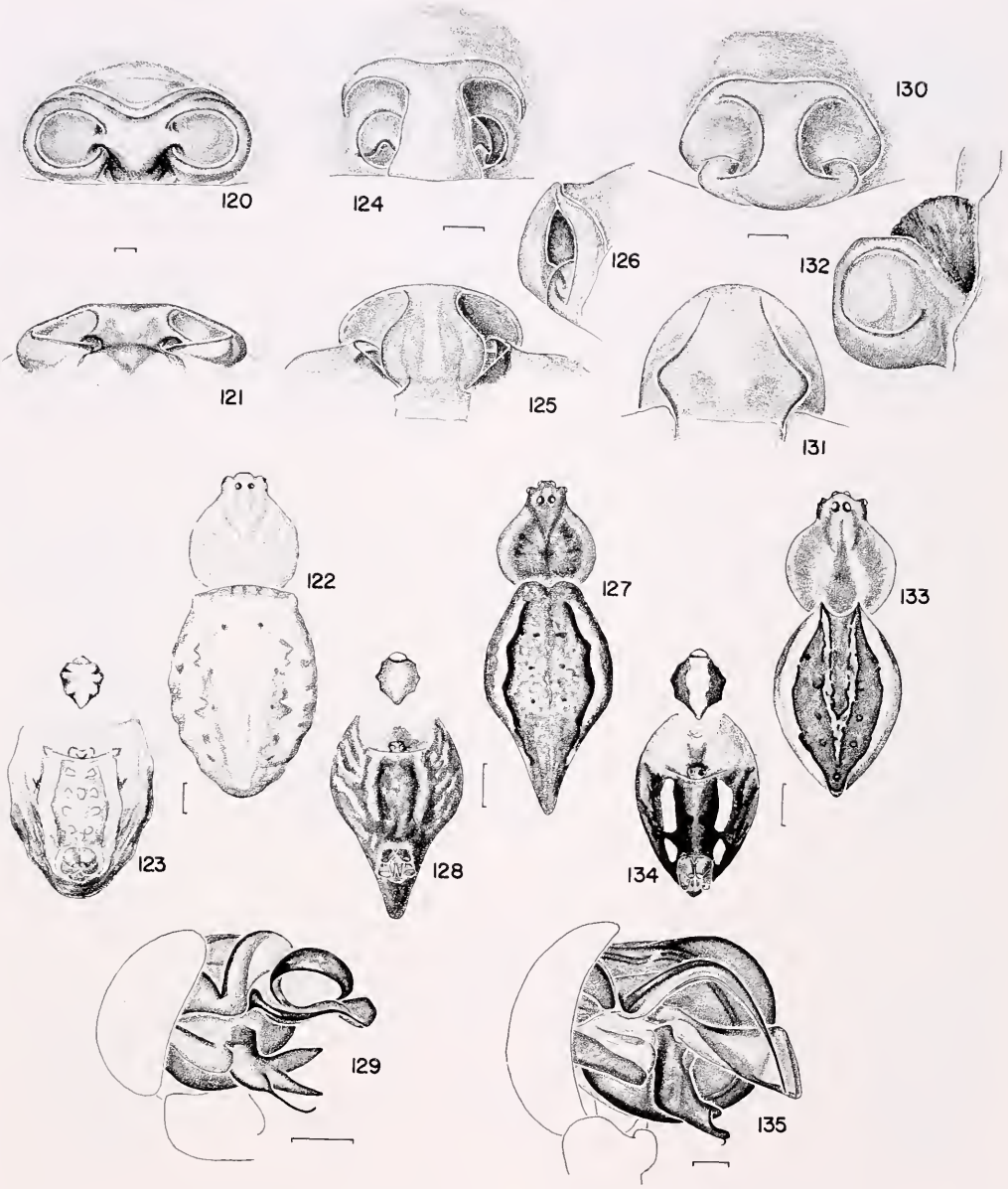
Argiope ocyaloides L. Koch

Figures 124–129; Map 4

Argiope ocyaloides L. Koch, 1871: 30, pl. 2, fig. 8, ♀. Female from Port Mackay [near Townsville, Queensland] in the Godeffroy collection, Zoologisches Museum, Universität Hamburg, lost. Female from Rockhampton, Queensland in the L. Koch collection of the British Museum, Natural History, here designated neotype, examined. Roewer, 1942: 742. Bonnet, 1955: 692.

Note. A female from Redlynch, Queensland, Australia, and a male from Proserpine, Queensland were illustrated.

Diagnosis. This small species resembles and has been confused with *A. doboensis* of New Guinea. It differs by having the septum and rims of the epigynum in the shape of a weakly sclerotized T (Fig. 124);



Figures 120–123. *Argiope bullocki* Rainbow, female. 120. Epigynum, ventral. 121. Epigynum, posterior. 122. Carapace and abdomen. 123. Sternum and abdomen.

Figures 124–129. *Argiope ocyaloides* L. Koch. 124–128. Female. 124. Epigynum, ventral. 125. Epigynum, posterior. 126. Epigynum, lateral. 127. Carapace and abdomen. 128. Sternum and abdomen. 129. Left male palpus, mesal.

Figures 130–135. *Argiope doboensis* Strand. 130–134. Female. 130. Epigynum, ventral. 131. Epigynum, posterior. 132. Epigynum, lateral. 133. Carapace and abdomen. 134. Sternum and abdomen. 135. Left male palpus, mesal.

Scale lines. 0.1 mm, except Figures 122, 123, 127, 128, 133, 134, 1.0 mm.

that of *A. doboensis* is an upside-down T. The male differs by having the embolus of the palpus coiled back on itself (Fig. 129), as is that of *A. probata*.

Records. AUSTRALIA: *Queensland.* ♀ (NMW); Cairns, 14 Oct. 1914, ♀ (W. M. Wheeler, MCZ); Redlynch, 18 Oct. 1938, ♀ (R. G. Wind, MCZ); Rochedale, 15 Dec. 1973, ♀♀ (R. Raven, QMB); Proserpine, 17 Aug. 1971, ♀, ♂ (N. C. Coleman, QMB).

Argiope doboensis Strand

Figures 1, 2, 130–135; Map 4

Argiope doboensis Strand, 1911b: 144, pl. 4, fig. 6, ♀ juv. Juvenile holotype from Wamar Island in forest between Dobo and Vezagil, Indonesia [Aru Isls.] in the Senckenberg Museum, Frankfurt, examined.

Argiope ocyaloides:—Chrysanthus, 1971: 14, figs. 13–16. M. H. Robinson and Lubin, 1979: 116, fig. 7 (web photo). M. H. Robinson and B. Robinson, 1980: 10, 51, 104–109, 192–193, figs. 52–54, ♀♂. Misidentification; not *A. ocyaloides* L. Koch.

Note. The female illustrated came from Madang, the male from Wau, Papua New Guinea.

Diagnosis. Argiope doboensis, like *A. ocyaloides*, is much smaller than most *Argiope* species, only about 7 mm total length. The female is readily recognized by the three pointed extensions on the abdomen, two anteriorly and one blunt one posteriorly (Fig. 133). The abdomen also has white bands on each side of the dorsum; the venter a pair of exclamation marks (Fig. 134). Unlike the Australian *A. ocyaloides*, the septum and posterior plate of the epigynum form an upside-down T in ventral view, and the openings are under a transverse slit on each side (Fig. 130).

The male, only slightly smaller than the female, has similar coloration on the abdomen, and is armed with strong macrosetae on the first and second patella and tibia. The abdomen is shield-shaped with points indistinct. Unlike *A. ocyaloides*, the embolus is evenly tapered to the tip and not coiled; the median apophysis has two prongs with the spur near the tip of the mesal one (Fig. 135).

Natural History. The web, like that of *Herennia*, is found on the trunks of trees, most common on *Araucaria*. Trunk projections support the web. Unlike the web of *Herennia*, it is not curved; at its closest it is 2 to 3 cm from the trunk (M. H. Robinson and Lubin, 1979). Courtship and mating is described in M. H. Robinson and B. Robinson, 1980.

Records. NEW GUINEA: *West Irian* [Djaya Pura]. Maffin Bay, Sept. 1944, ♀ (E. S. Ross, CAS). *Papua New Guinea.* Morobe Distr.: Wau, ♀♂ (MCZ); Bulolo, 18 Aug. 1970, ♀ (M. Gray, AMS).

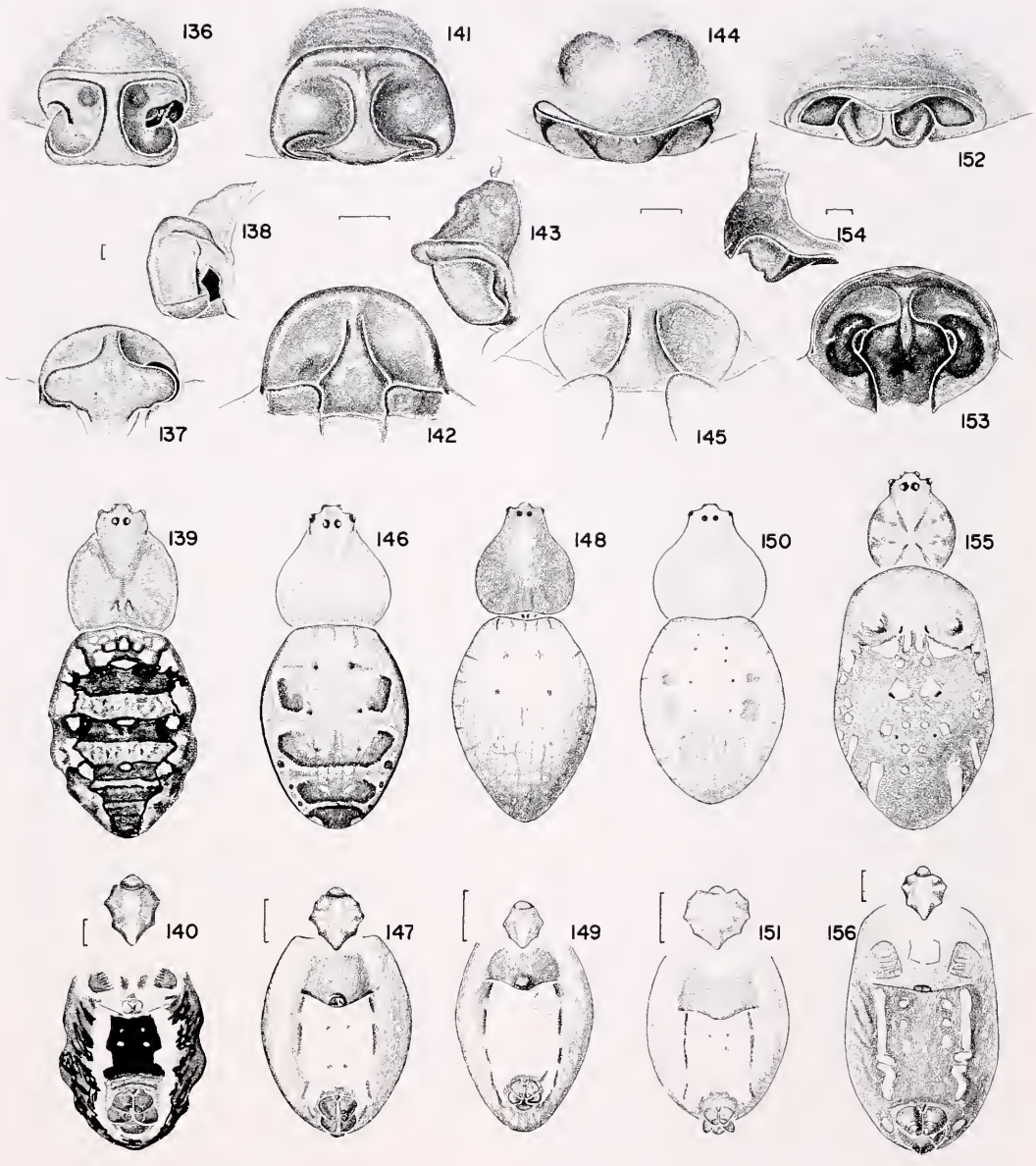
Argiope dietrichae new species

Figures 136–140; Map 4

Holotype. Female from Pyramid Pool Cave, Western Australia, 30′ [10 m] above water, 5 June 1970 [22°17′S 118°19′W] in the Western Australian Museum, Perth. The species is named after Amalie Dietrich, 19th century collector of spiders for Godeffroy.

Description. Female paratype from Dales Gorge. Carapace brown streaked with light colored down. Sternum with a median posterior white mark. Legs light brown with darker spots and bands. Dorsum of abdomen with a folium surrounded by light dots. Folium enclosing transverse bands, spotted. Venter with usual *Argiope* pattern. Anterior lateral eyes 0.8 diameter of anterior medians. Posteriors subequal to anterior medians. Anterior median eyes 1.3 diameters apart, 1.5 from laterals. Posterior median eyes 1.5 diameters apart, 2.5 from laterals. Abdomen slightly lobed on sides (Fig. 139). Total length, 13.5 mm. Carapace, 5.3 mm long, 4.5 mm wide. First femur, 9.4 mm; patella and tibia, 10.2 mm; metatarsus, 9.8 mm; tarsus, 2.3 mm. Second patella and tibia, 10.1 mm; third, 5.2 mm; fourth, 8.8 mm.

Diagnosis. Argiope dietrichae differs from *A. ocyaloides*, *A. doboensis*, and *A. katherina* by having a narrower rim and septum of the epigynum (Fig. 136), and in having the posterior plate much wider than long in posterior view (Fig. 137). The



Figures 136–140. *Argiope dietrichae* n. sp., female. 136. Epigynum, ventral. 137, Epigynum, posterior. 138. Epigynum, lateral. 139. Carapace and abdomen. 140. Sternum and abdomen.

Figures 141–151. *Argiope chloreis* Thorell, female. 141. Epigynum, ventral. 142, 145. Epigynum, posterior. 143. Epigynum, lateral. 144. Epigynum, anteroventral. 141–143. (Western New Guinea). 144, 145. (Sumatra). 146, 148, 150. Carapace and abdomen. 147, 149, 151. Sternum and abdomen. 146, 147. (Western New Guinea). 148, 149. (Sumatra). 150, 151. (Celebes).

Figures 152–156. *Argiope thai* n. sp., female. 152. Epigynum, ventral. 153. Epigynum, posterior. 154. Epigynum, lateral. 155. Carapace and abdomen. 156. Sternum and abdomen.

Scale lines. 0.1 mm, except Figures 139, 140, 146–151, 155, 156, 1.0 mm.

abdomen lacks an anterior projection and a posterior extension behind the spinnerets (Fig. 139).

Variation. The septum of the epigynum of one specimen from Wotjulum Mission is considerably wider than that illustrated from Dales Gorge. Specimen from Tanami Bone Hole, N.T. has the abdomen entire and the openings in ventral view are circles. Four specimens from Kimberley Distr. differ by having the posterior plate of the epigynum triangular and the lips of the openings circular. The abdomen is less lobed.

Paratypes. AUSTRALIA: *Western Australia.* Dales Gorge, 625 m, 10 Oct. 1962, ♀, juv. (E. S. Ross and D. Q. Cavagnaro, CAS); Wotjulum Mission via Derby, Oct. 1955, 2♀ (A. Douglas, WAM); 4♀ (WAM). *Northern Territory.* Tanami Govt. Borehole, July 1971, ♀ doubtful determ. (J. Hodgson, CSIRO).

Argiope chloreis Thorell

Figures 141–151; Map 4

Argiope chloreis Thorell, 1877: 368. Juvenile female holotype from Kendari, Celebes in the Museo Civico di Storia Naturale, Genova, examined. Roewer, 1942: 738. Bonnet, 1955: 684.

Argiope pumila Thorell, 1890: 99. Female syntype from Sungeibulu, Sumatra in the Museo Civico di Storia Naturale, Genova, examined. Roewer, 1942: 738. Bonnet, 1955: 693. NEW SYNONYMY.

Argiope chloreides Chrysanthus, 1961: 197, figs. 5–8, ♀. Female holotype from Mindiptana, West New Guinea in the Rijksmuseum van Natuurlijke Historie, Leiden, examined. NEW SYNONYMY.

Notes. The penultimate female of *A. chloreis* (Figs. 150, 151) probably belongs to the same species as *A. pumila* (Figs. 148, 149). They have similar white venter of the abdomen. The dorsal markings of *A. pumila* have disappeared (Fig. 148). The sternum of *A. chloreis* is noticeably larger (Fig. 151) than that of *A. pumila* (Fig. 149); that of the type specimen of *A. chloreides* is intermediate in size (Fig. 147). Figures 141–143, 146, 147 were prepared from the holotype of *A. chloreides*, the best preserved of these specimens. Chrysanthus indicated that *A. chloreides* differed by lacking macrosetae on the ventral side of the tibia I and II. But examination of the holotype showed that they had broken off.

Diagnosis. Argiope chloreis has very distinct coloration: the dorsum of the abdomen has light bordered dark patches (Fig. 146); the venter a median rectangular white area, bordered on each side by a narrow, broken longitudinal dark line (Figs. 147, 149, 151). The abdomen lacks the anterior projection of *A. doboensis.* Circling the abdomen on the sides is a distinct line bordering a much lighter area on the dorsum, and a much darker area ventrally than on the dorsum. The epigynum is small and relatively flat (Figs. 141–145).

Distribution. Sumatra, Moluccas to New Guinea (Map 4).

Records. INDONESIA: *Moluccas.* Morotai Isl., Jan.–April 1945, ♀ (G. Banner, AMNH). *Sumatra.* Perdagangan [?], ♀ (E. Mjöberg, NRS). PAPUA NEW GUINEA: *East Sepik Distr.* Töpferfluss [Keram River], 21 April 1913, ♀ (Bürgers, ZMB). *Milne Bay Distr.* Modewa Bay, 32–40 km W of Samarai, 1956, ♀ (Archbold Exped., AMNH). *Madang Distr.* Finisterre Mts., Naho River Valley, Damanti, 1100 m, 2–7 Oct. 1964, imm. doubtful determ. (M. E. Bacchus, BMNH).

Argiope thai new species

Figures 152–156; Map 4

Holotype. Female in poor condition from Preuw, Chantaburi [Chathaburi], Thailand, 4 Jan. 1958 (N. Meinkoth) in the Museum of Comparative Zoology. The specific name is a noun in apposition, derived from the country of the type locality.

Description. Carapace light brown with dark brown irregular patches, covered with white setae. Sternum with median longitudinal white pigment band, dark on sides. Legs light brown with dark brown speckles. Dorsum of abdomen with indistinct white patches. Venter dark brown with two longitudinal lines and white

spots. Anterior lateral eyes 0.6 diameter of anterior medians; posterior median eyes 1.4 diameters; posterior laterals 1.2 diameters. Anterior median eyes their diameter apart, 1.5 from laterals. Posterior median eyes 1.2 diameters apart, 2 from laterals. Total length, 13.0 mm. Carapace, 3.7 mm long, 3.2 mm wide. First femur, 5.0 mm; patella and tibia, 5.2 mm; metatarsus, 5.0 mm; tarsus, 1.7 mm. Second patella and tibia, 6.3 mm.

Diagnosis. This species differs from other *Argiope* by having the second leg considerably longer than the first. The epigynum differs from all other *Argiope* by having the flange of the rim forming a lobe on each side of the depression (Fig. 152). The wide posterior plate fills the depression, and is hollowed out on each side of the septum (Fig. 153).

Argiope possoica Merian, new status

Figures 157–161; Map 4

Argiope celebesiana possoica Merian, 1911: 205. Female holotype from Posso Sea [Teluk Poso Bay], Celebes in the Naturhistorisches Museum, Basel, examined. Roewer, 1942: 738. Bonnet, 1955: 684.

Note. This species was described as a subspecies of *A. reinwardti.*

Diagnosis. Argiope possoica superficially resembles *A. modesta* in abdominal markings (Figs. 160, 161). The thick rim of the epigynum (Fig. 157) distinguishes *A. possoica* from *A. minuta. Argiope possoica* has "bottle brushes" on the ends of the tibiae, especially on the fourth legs.

Argiope perforata Schenkel

Figures 162–166; Map 4

Argiope perforata Schenkel, 1963: 135, fig. 79, ♀. Female holotype from Lunan fu city [Lung-ngan fu], Szetchuan, China in the Muséum National d'Histoire Naturelle, Paris, examined.

Note. The holotype is in poor condition. The illustrations were made from a specimen from Kwantung Province.

Diagnosis. The color pattern of the abdomen (Fig. 165) and the narrower septum in the epigynum (Fig. 162) separate *Argiope perforata* from *A. anasuja.*

Record. CHINA: *Kwantung Prov.* Kwantung City, Paiyunshan, 25 Aug. 1978, ♀ (T. Terada, ASEA).

Argiope anasuja Thorell

Figures 167–172, Map 4

Argiope ornata:—Simon, 1885: 34. Misidentification; not *A. ornata* Blackwall [=*Nephila antipodiana* (Walckenaer)].

Argiope anasuja Thorell, 1887: 162. New name for *A. ornata*:—Simon. One female lectotype, one female and one male paralectotype, and juveniles, all in poor physical condition, from Kulachee, British India [Kulachi, Pakistan] in the Muséum National d'Histoire Naturelle, Paris, here designated. Gravely, 1921: 412, fig. 3a, ♀. Roewer, 1942: 737. Bonnet, 1955: 672.

Argiope plagiata Karsch, 1891: 279, pl. 10, fig. 5, ♀. Three female syntypes from Minicoy Islands, Indian Ocean in the Zoologisches Museum, Humboldt Universität, Berlin, examined. NEW SYNONYMY.

Note. The illustrations were made from a specimen from Karnatake, India.

Diagnosis. The genitalia of this small species resemble those of *A. minuta, A. doboensis,* and *A. perforata.* The species, however, is larger than these three. The female has a pair of anterolateral tubercles and transverse bands on the dorsum of the abdomen (Fig. 170). The rims of the epigynum have a flange with a lateral tooth providing an anterior lip to the openings (Fig. 167); the openings are posterior, within the posteriorly extended septum (Figs. 167, 168).

The male has the embolus strongly curved distally, and longer than that of *A. minuta* and *A. doboensis.* The median apophysis has the filamentous spur attached near the middle (Fig. 172).

Distribution. Pakistan, India, Sri Lanka Maldives and Cocos-Keeling Islands (Map 4).

Records. INDIA: *West Bengal.* Tarkhola, Kalimpong Distr., 325 m, Aug. 1958, juv., ♀ (M. L. Bristol, MCZ); Kanchrafara [Kanchrapara ?], July 1944, ♀♀ (M. Cazier,

AMNH). *Karnataka*. Bangalore, 300 m, Nov. 1979, ♀, ♂ (W. Eberhard, MCZ); Dandeli, 530 m, Nov. 1979, ♀ (W. Eberhard, MCZ). *Tamil Nadu*. 5 km W Rajapalayam, Ayyanar Falls, 350 m, Nov. 1979, ♀, ♂ (W. Eberhard, MCZ). *Madras*. Madras, 27 Dec. 1969, ♀ (M. Gray, AMS); Sept. 1948, ♀ (N. Haarler, ZMK); Vellore, ♀, ♂ (M. Löwenthal, ZMK); Mandapam Camp, 3 Oct. 1951 (H. Lemche, ZMK). *Maharashtra*. Bombay, ♀♀ (HCO). SRI LANKA: "Ceylon," ♀ (Reimoser, NMW); ♀ (Bedemann, NMW); Colombo, 23 Jan. 1927, ♀ (J. G. Myers, MCZ); Yala, Oct. 1979, ♂ (W. C. Sedgwick, SC); Kagalu Beach Hotel, Galle, Oct. 1979, ♀ (W. C. Sedgwick, SC). INDIAN OCEAN: *Cocos-Keeling Islands*. West Isl., 11 Nov. 1964, ♀; June 1952, ♀; scrub near Tanjong Klirkil, May 1952, 2♀, ♂; south end West Isl., 12 Nov. 1964, 2♀ (all T. G. Campbell, CSIRO). MALDIVES: *Ari Atoll*. Insel Fusdu, 18 April 1958, ♀ (Klausewitz, SMF). *Addu Atoll*. 23 Jan. 1958, ♀ (SMF); Wadewaru Isl., 7 April 1958, ♀ (S. Gerlach, SMF). *Maté Atoll*. 3♀ (SMF). *Rastú Atoll*. Insel Weligandu, 8 March 1958, ♀♀♂ (Klausewitz, SMF).

Argiope halmaherensis Strand

Figures 173–177; Map 4

Argiope halmaherensis Strand, 1907b: 65, pl. 171, fig. 4, ♀. Female holotype from Halmahera Isl., Moluccas, in the Staatliches Museum für Naturkunde, Stuttgart, destroyed in the last war. No specimens in Görlitz. Roewer, 1942: 738. Bonnet, 1955: 686.

Argiope mindiptanensis Chrysanthus, 1961: 195, figs. 1–4, ♀. Female holotype from Mindiptana, West Irian [New Guinea] in the Rijksmuseum van Natuurlijke Historie, Leiden, examined. NEW SYNONYMY.

Note. Strand provided three primitive sketches of the epigynum which show the unusual proportions. Strand's specimen had three equally wide yellow-white transverse bands on the abdomen dorsum, separated by thin lines, and was dark brown posteriorly. While Strand's description fits, I believe his figure 4a to be on its side, figure 4b to be the epigynum from posterior view, 4c the epigynum from ventral view with the posterior part of the epigynum hidden by the abdomen. The illustrations (Figs. 173–177) were made from the holotype of *A. mindiptanensis*.

Diagnosis. The female of this small sized *Argiope* can be separated from others by the three pairs of dorsal white patches on the abdomen (Fig. 176), and by the epigynum. The epigynum is trapezoidal, longer than wide, widest anteriorly (Fig. 173). Like *A. anasuja*, the posterior plate forms a bowl, and the rim has a flange.

Variation. The only other specimen in collections from the Sepic River had the epigynum more square.

Records. PAPUA NEW GUINEA: Kaiserin Augustafluss Exped. [Sepic River], July 1912, ♀ (Bürger, ZMB).

Argiope niasensis Strand

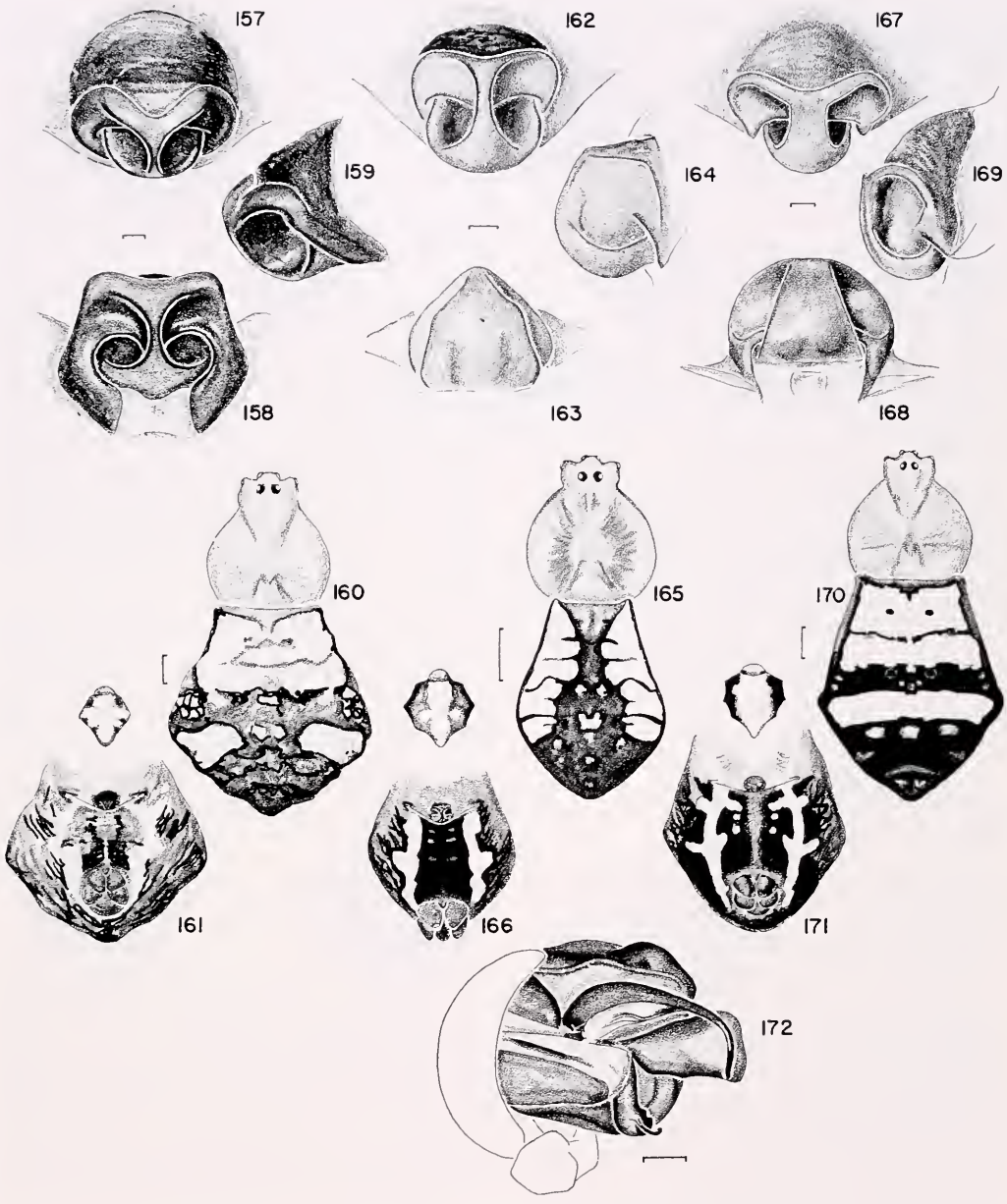
Figures 178–182; Map 4

Gea spinipes:—Simon, 1905: 62. Misidentification; not *G. spinipes* (L. Koch).

Argiope niasensis Strand, 1907b: 56, figs. 1–3, ♀. Female holotype from Joenoeng-Sitoli, Nias Island (west of Sumatra) in the Staatliches Museum für Naturkunde, Stuttgart, destroyed during the last war. No specimens in Görlitz Museum. Female neotype here designated from Bogor in the Museum of Comparative Zoology, Harvard University.

Note. The small sketch of the epigynum provided by Strand is diagnostic. Strand's size fits. However, Strand's specimen had three transverse white bands on the abdomen like *A. reinwardti* (Strand, 1907: fig. 3). The neotype from Bogor was illustrated.

Diagnosis. The abdomen of the female is pentagonal, widest posteriorly with small anterior humps (Fig. 181). The dorsal abdominal markings have unfortunately washed out. The epigynum, unlike others, has a large septum, trapezoidal in ventral view, widest posteriorly (Fig. 178). The rim borders a short, wide bulge. Posteriorly the septum continues into the pos-



Figures 157–161. *Argiope possoica* Merian, female. 157. Epigynum, ventral. 158. Epigynum, posterior. 159. Epigynum, lateral. 160. Carapace and abdomen. 161. Sternum and abdomen.

Figures 162–166. *Argiope perforata* Schenkel, female. 162. Epigynum, ventral. 163. Epigynum, posterior. 164. Epigynum, lateral. 165. Carapace and abdomen. 166. Sternum and abdomen.

Figures 167–172. *Argiope anasuja* Thorell. 167–171. Female. 167. Epigynum, ventral. 168. Epigynum, posterior. 169. Epigynum, lateral. 170. Carapace and abdomen. 171. Sternum and abdomen. 172. Left male palpus, mesal.

Scale lines. 0.1 mm, except Figures 160, 161, 165, 166, 170, 171, 1.0 mm.

terior plate which has nearly parallel sides (Fig. 179).

Distribution. Sumatra, Java (Map 4).

Records. INDONESIA: *Java.* Buitenzorg [Bogor], 1904, ♀ (H. Jenson, ZMK); ♀ (MCZ); Tjibodas [Cibodas], 25–28 March 1904, ♀ (K. Kraepelin, ZMK).

Argiope takum Chrysanthus

Figures 183–187; Map 4

Argiope takum Chrysanthus, 1971: 17, figs. 23–25, ♀. Female holotype from Kamp Wifob, Takum, West New Guinea [Djaya Pura], 10 Aug. 1959 (Star Mts. Expedition) in the Rijksmuseum van Natuurlijke Historie, Leiden, examined.

Diagnosis. Argiope takum differs from other *Argiope* species by the shape of the epigynum and the shape of the abdomen. The septum of the epigynum hangs and widens posteriorly into a bowl-shaped posterior plate (Figs. 183–185); the dorsum of the abdomen has indistinct paired patches (Fig. 186), the venter two white exclamation marks (Fig. 187).

Argiope mascordi new species

Figures 188–192; Map 4

Holotype. Female from Mt. Garnet, Queensland, 25 Feb. 1972 (N. C. Coleman), #KS 101 in the Australian Museum, Sydney. This species is named after Ramon Mascord, collector and author of books on Australian spiders.

Description. Carapace yellow-brown with dark brown marks and covered by white down. Sternum very dark on sides, a light longitudinal band through middle (Fig. 192). Legs contrastingly banded, darker bands wider than light. Dorsum of abdomen with a folium having jagged outline (Fig. 191). Venter with two white lines, black in between, enclosing paired white spots (Fig. 192). Anterior lateral eyes 0.5 diameter from anterior medians. Posterior median eyes 1.1 diameters; posterior laterals subequal to anterior median eyes. Anterior median eyes their diameter apart, 1.2 from laterals. Posterior median eyes their diameter apart, 2.0 from laterals. The height of the clypeus equals the diameter of the anterior median eyes. The abdomen is oval with indistinct dorsal anterior humps. Total length, 9.5 mm. Carapace, 3.7 mm long, 3.2 mm wide. First femur, 5.2 mm; patella and tibia, 5.8 mm; metatarsus, 5.3 mm; tarsus, 1.5 mm. Second patella and tibia, 5.6 mm; third, 3.2 mm; fourth, 5.1 mm.

Diagnosis. Argiope mascordi differs from *A. keyserlingi, A. caledonia,* and *A. kochi* by the oval shape of the abdomen, by having a dorsal folium (Fig. 191), and by being smaller in size. The epigynum in posterior view is more pointed ventrally (Fig. 189) than the squarish epigynum of *A. keyserlingi* or the round one of *A. caledonia. A. mascordi* lacks the lateral lobes on either side of the epigynum as found in *A. keyserlingi.*

The palpus illustrated by Fig. 193 may be of the male of this species or *A. kochi.*

Paratypes. AUSTRALIA: *Queensland.* Almaden, March 1929, ♀ (W. D. Campbell, AMS); Chillagoe Caves area, 18 July 1978, ♀ (R. Mascord, AMS); 21 km E Croydon, 150 m, 4 Nov. 1962, ♀ (E. S. Ross, D. Q. Cavagnaro, CAS).

Argiope keyserlingi Karsch

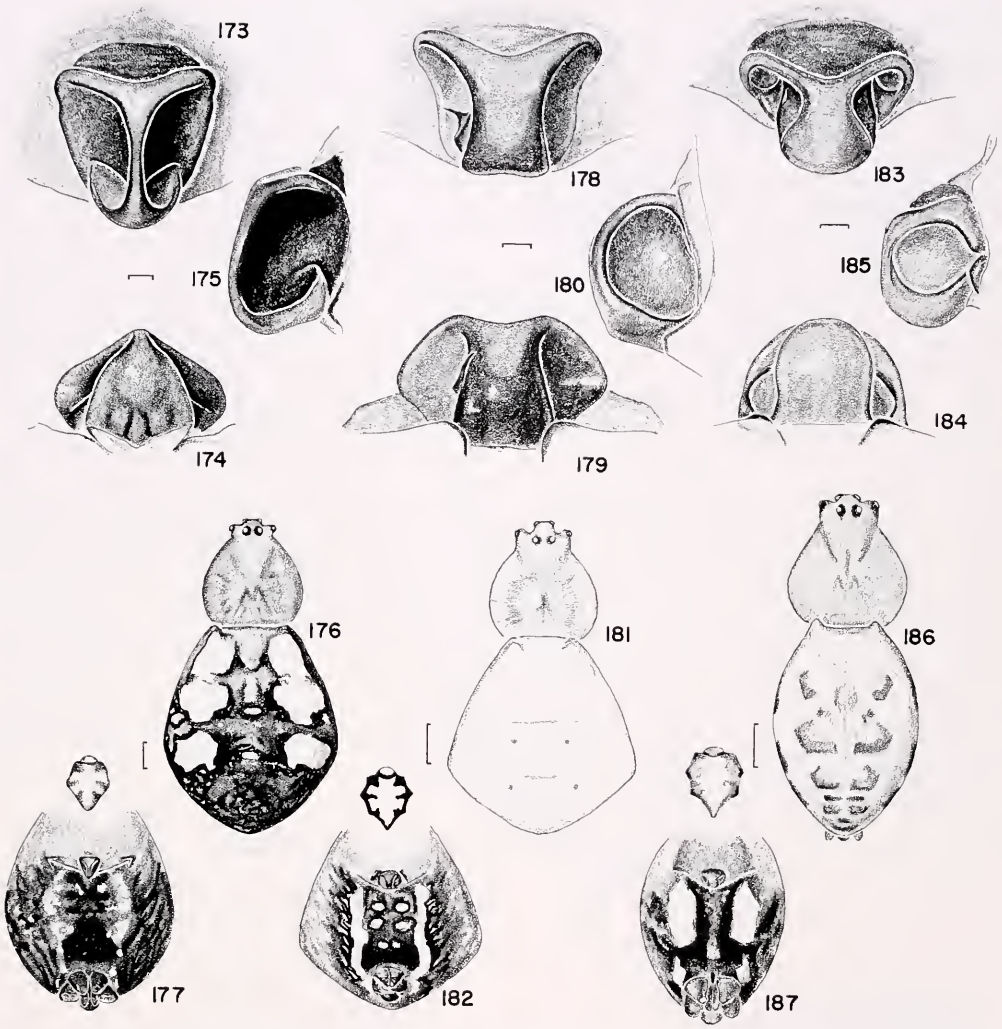
Figures 194–199; Map 4

Argiope aetherea:—Keyserling, 1865: 803, pl. 19, figs. 1, 2, ♀. Female specimen from Woollongong [New South Wales], lost. Misidentification; not *A. aetherea* (Walckenaer).

Argiope keyserlingi Karsch, 1878: 789. New name for *A. aetherea*:—Keyserling, 1865, misidentification.

Neotype. Female from Canterbury near Sydney, New South Wales, labeled "*Argiope aetherea,* K57683, 1 April 1928" by Rainbow, in the Australian Museum, Sydney.

Diagnosis. The female differs from other species, particularly *Argiope aetherea,* by the epigynum having a flat flange on the rim, with a lobe on each side posteriorly (in ventral view) (Fig. 194). In posterior view the epigynum shows the wide, flat flange and a nearly circular opening



Figures 173–177. *Argiope halmaherensis* Strand, female. 173. Epigynum, ventral. 174. Epigynum, posterior. 175. Epigynum, lateral. 176. Carapace and abdomen. 177. Sternum and abdomen.

Figures 178–182. *Argiope niasensis* Strand, female. 178. Epigynum, ventral. 179. Epigynum, posterior. 180. Epigynum, lateral. 181. Carapace and abdomen. 182. Sternum and abdomen.

Figures 183–187. *Argiope takum* Chrysanthus, female. 183. Epigynum, ventral. 184. Epigynum, posterior. 185. Epigynum, lateral. 186. Carapace and abdomen. 187. Sternum and abdomen.

Scale lines. 0.1 mm, except Figures 176, 177, 181, 182, 186, 187, 1.0 mm.

quite far dorsally (Fig. 195). The abdomen is more rounded than the pentagonal one of *A. aetherea* (Figs. 197, 198).

The male differs from *A. aetherea* by the much smaller embolus: the base of the embolus has a prong with parallel sides; the tip has a neck and a distal expansion. The median apophysis has the spur originating from near its bend (Fig. 199).

Variation. Females vary 9 to 16 mm total length.

Natural History. The only record with

natural history data is one female from Careel Bay, New South Wales, from a salt marsh. Most illustrations of the St. Andrew's spider seem to be this species (Clyne, 1969: figs. 153–159; Mascord, 1970: fig. 132).

Distribution. Queensland, New South Wales coast, Lord Howe Island (Map 4).

Paratypes. AUSTRALIA: *Queensland.* Atherton, 3♀ (NRS); Brisbane, ♀ (NMW), ♀♀ (HCO); East Brisbane, 1 June 1911, ♀ (H. Buch, ZMK); Rockhampton, ♀♀ (HCO); Molangool, ♀ (AMS). *New South Wales.* Wyangarie, ♀♂ (AMS); Mascot, 24 Nov. 1966, ♂ (AMS); North Ryde, 22 Nov. 1966, ♂ (D. A. Doolan, AMS); Regent's Park, 26 April 1978, ♀ (AMS); Currawong, 2 Oct. 1966, ♀ (R. Mascord, AMS); 12 March 1966, ♀ (AMS); Roseville, 3 Nov. 1929, ♀ (F. W. Rodda, AMS); Careel Bay, 4 Dec. 1972, ♀ in salt marsh (D. Wilson, AMS); Darlinghurst, 19 Dec. 1973, ♀ (R. Banuelos, AMS); Sydney, ♀ (AMS); Tamworth, ♀ (AMS); The Basin, 12 March 1966, ♀ (AMS); Elanora, near Narrabeen, 100 m, 3 Dec. 1962, ♀♂ (E. S. Ross, D. G. Cavagnaro, CAS); Sylvania, 20 Dec. 1962, ♀ (E. S. Ross, D. G. Cavagnaro, CAS); S of Arroca Beach, Bouddi National Park, 9 Jan. 1978, ♀ (E. I. Schlinger, EMB); Sydney, 1884 (NMW). *Lord Howe Island.* ♀♀♂♂, Feb. 1971 (AMS).

Argiope kochi new species

Figures 200–204; Map 4

Argiope aemula:—Mascord, 1980, pl. 24, fig. 2 (photograph). Misidentification; not *A. aemula* (Walckenaer).

Holotype. Female from Edmonton, northern Queensland, 13 June 1969 (N. C. Coleman), KS 6193 in the Australian Museum, Sydney. The species is named after Ludwig Koch, who described many *Gea* and *Argiope* species from Australia 100 years ago.

Description. Carapace beige, covered by white down. Sternum with sides dark, median area light (Fig. 204). Legs brown, not banded; some darker patches on underside. Dorsum of abdomen white with thin black transverse lines; posterior black, reticulated (Fig. 203). Venter strikingly marked with black and white bands of equal width (Fig. 204). Anterior lateral eyes 0.5 diameter of anterior medians. Posterior median eyes 1.2 diameters, posterior lateral eyes 1.2 diameters of anterior medians. Anterior median eyes 1.2 diameters apart, two from laterals. Posterior median eyes 1.5 diameters apart, three from laterals. The shape of the abdomen is pentagonal. Total length, 8.2 mm. Carapace, 3.7 mm long, 3.3 mm wide. First femur, 5.2 mm; patella and tibia, 5.6 mm; metatarsus, 5.0 mm; tarsus, 1.4 mm. Second patella and tibia, 5.4 mm; third, 3.0 mm; fourth, 4.6 mm.

Diagnosis. This species differs from other Australian *Argiope* species by the contrasting ventral abdominal markings (Fig. 204). The epigynum has a wide flange posterior to the rim and a slit-like opening (Figs. 200, 201).

The palp illustrated by Fig. 193 may belong to a male of this species or *A. mascordi.*

Records. AUSTRALIA: *Queensland.* Cape York Peninsula, Sept., ♀ (E. Mjöberg, NRS).

Argiope minuta Karsch

Figures 205–210; Map 4

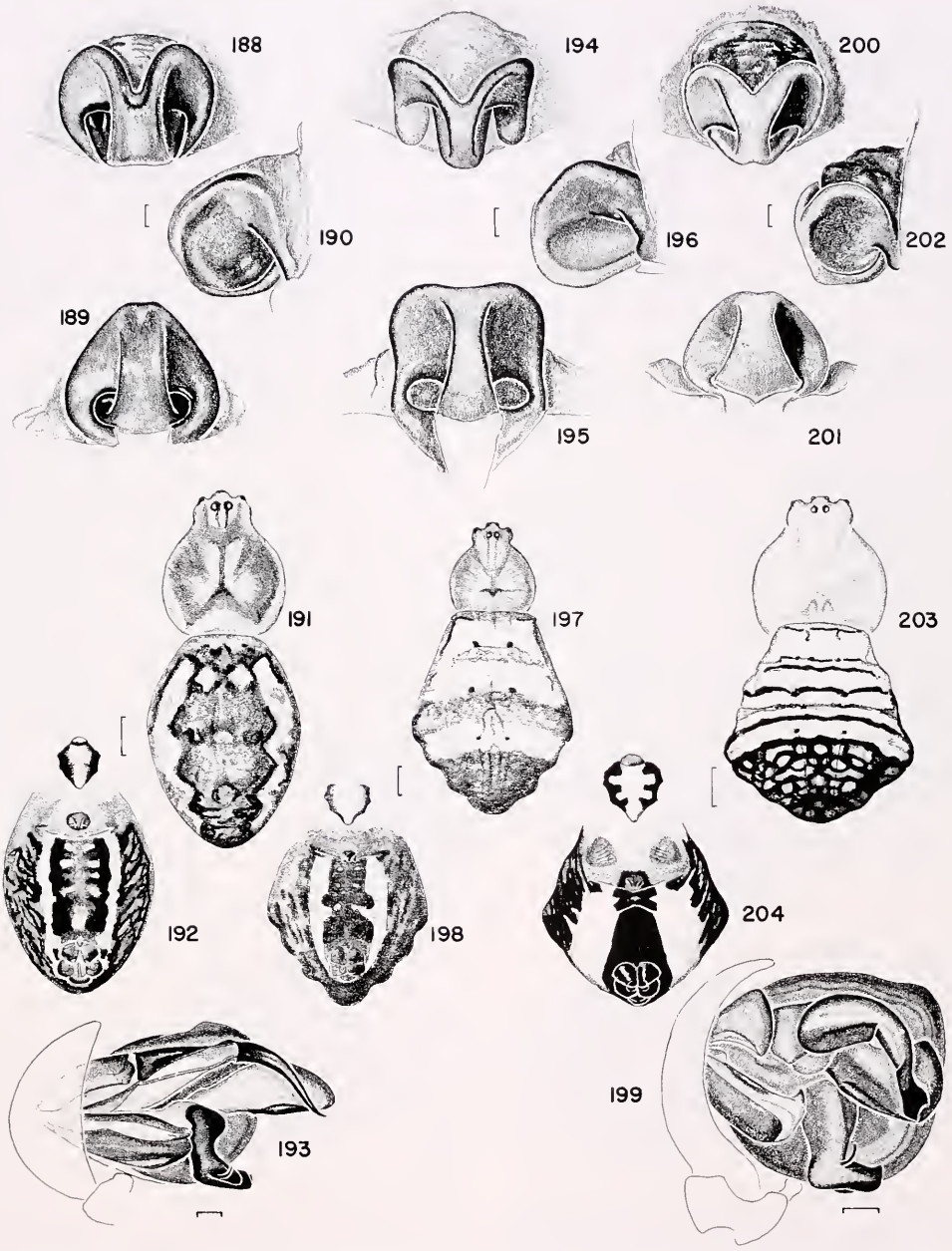
Argiope minuta Karsch, 1879: 67. Juvenile specimens from Japan in the Zoologisches Museum, Humboldt Universität, Berlin, examined. Bösenberg and Strand, 1906: 194, pl. 1, fig. 16, pl. 11, figs. 218, 222, ♀, ♂. Roewer, 1942: 736. Bonnet, 1955: 69. Yaginuma, 1960: 145, pl. 25, fig. 145, ♀. Song, 1980: 99, fig. 45, ♀.

Coganargiope (*Micrargiope*) *minuta*:—Kishida, 1936: 19.

? *Argiope shillongensis* Sinha, 1951: 75, fig. 1, ♀. Female holotype from Shillong, Assam, India in the Zoological Survey of India collection, unavailable. DOUBTFUL NEW SYNONYMY.

Note. The illustrations were made from specimens from Checkiang Prov., China. The illustration of Sinha's *A. shillongensis* appears to be that of *A. minuta.* If it is, it would extend the range of the species to Assam.

Diagnosis. The female of this small species has two transverse, wide dark



Figures 188–192. *Argiope mascordi* n. sp., female. 188. Epigynum, ventral. 189. Epigynum, posterior. 190. Epigynum, lateral. 191. Carapace and abdomen. 192. Sternum and abdomen.

Figure 193. *Argiope mascordi* n. sp. or *A. kochi* n. sp., left male palpus, mesal.

Figures 194–199. *Argiope keyserlingi* Karsch. 194–198. Female. 194. Epigynum, ventral. 195. Epigynum, posterior. 196. Epigynum, lateral. 197. Carapace and abdomen. 198. Sternum and abdomen. 199. Left male palpus, mesal.

Figures 200–204. *Argiope kochi* n. sp., female. 200. Epigynum, ventral. 201. Epigynum, posterior. 202. Epigynum, lateral. 203. Carapace and abdomen. 204. Sternum and abdomen.

Scale lines. 0.1 mm, except Figures 191, 192, 197, 198, 203, 204, 1.0 mm.

bands across the dorsum of the abdomen, each enclosing some white spots (Fig. 208). Anteriorly the abdomen has small anterior lateral humps. The rim of the anterior bulge of the epigynum has a flange which encloses the openings (Figs. 205, 206). Unlike *A. anasuja*, the septum is narrow and widens posteriorly into a transverse posterior plate (Fig. 206).

The median apophysis has its inside branch hanging "down"; the conductor is partially wrapped around the tip of the embolus (Fig. 210).

Distribution. Japan, China (Map 4).

Records. JAPAN: *Hyogo Pref.* Siyodenyama, Setsu, Sept. 1895, ♀ (T. Lenz, ZMH). *Wakayama Pref.*, Hatakejima [Hatake-Yama Mt.], Shirahama, 31 Oct. 1973, ♀ (W. C. Sedgwick, SC); *Mie Pref.*, 23 Oct. 1951, ♀♀ (AMNH). *Osaka Pref.* Osaka, Tennoji, Aug. 1895, ♀ (T. Lenz, ZMH); Osaka, 18 Aug. 1956, ♂ (T. Yaginuam, MCZ). *Nara Pref.* Yoshino, 29 Aug. 1976, ♀ (T. Yaginuma, MCZ). SOUTH KOREA: Mt. Chiri [Chi-San], 8 Aug. 1959, ♀ (K. Paik, AMNH). TAIWAN: Tai Pei, Aug. 1957, ♀ (Wang, AMNH). CHINA: Chekiang Prov., Mokanshan [Mo-Kan Shan Mt.], N Gist Gee of Soochow, ♀♂ (Song, 1980) (MCZ). HONG KONG: Peak, 22 Sept. 1931, ♀ (R. Sherriffs, ZMK).

Argiope katherina new species

Figures 211–216; Map 4

Holotype. Female and juvenile and male paratypes from Katherine Gorge, Northern Territory, Australia, Dec. 1980 (R. R. Jackson), in the Queensland Museum, Brisbane, no. S904. The specific name is a noun in apposition after the type locality.

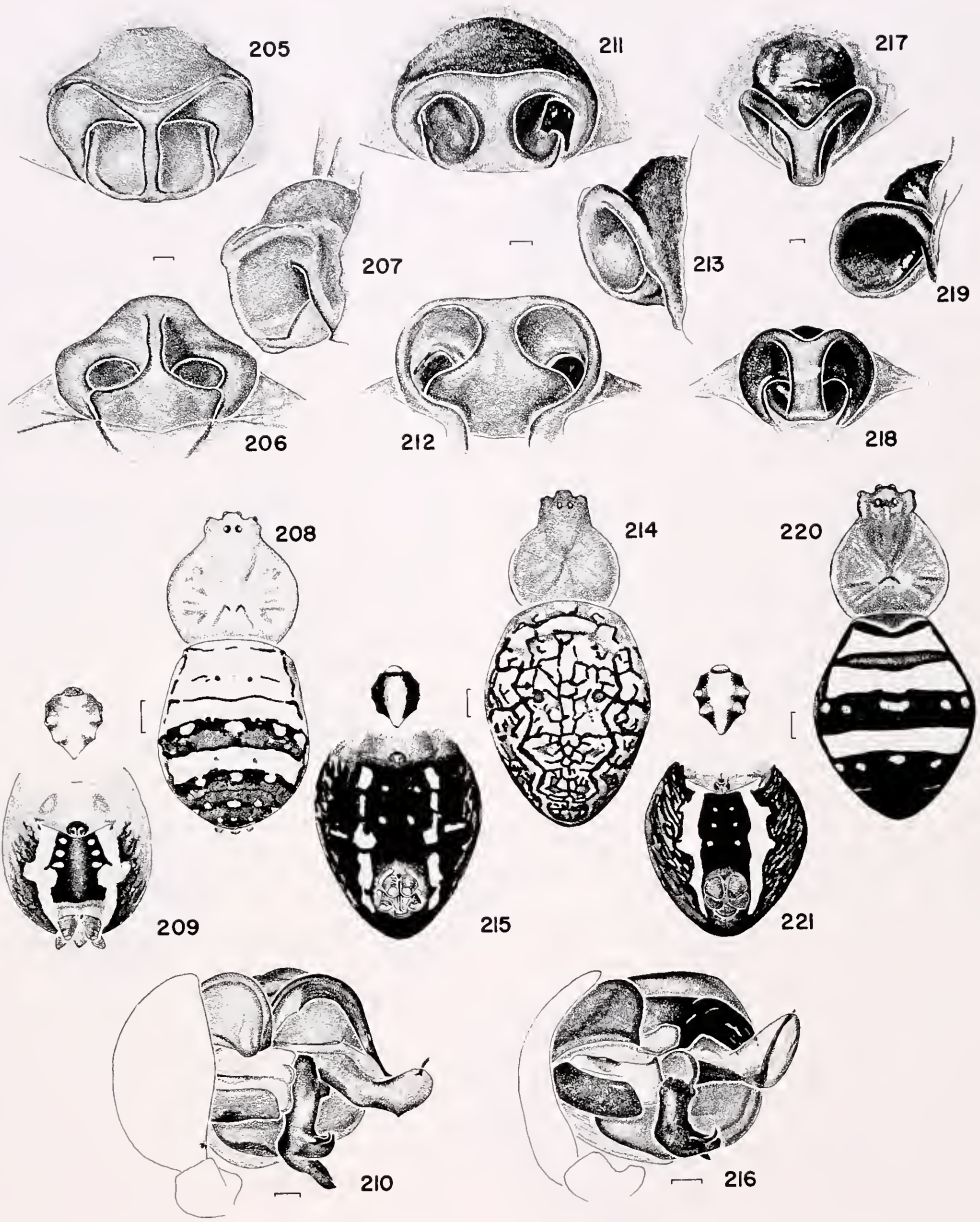
Description. Carapace dark brown, light around edge and thinly covered with white down. Sternum black with a median longitudinal mark (Fig. 215). Coxae black, each with a small white spot. Palpi white. Legs dark brown; distal end of tibiae and metatarsi black; tarsi black. Dorsum of abdomen with diagnostic reticulate pattern (Fig. 214). Venter black with slender white marks (Fig. 215). Secondary eyes subequal in size to anterior median eyes except for anterior laterals, 0.7 diameter of anterior medians. Anterior median eyes about their diameter apart. Posterior median eyes about their diameter apart, 1.5 from laterals. The abdomen is oval in outline. Total length, 14.5 mm. Carapace, 5.0 mm long, 4.2 mm wide. First femur, 7.4 mm; patella and tibia, 8.2 mm; metatarsus, 7.6 mm; tarsus, 1.9 mm. Second patella and tibia, 8.0 mm; third, 4.6 mm; fourth, 7.7 mm.

Male. Carapace light olive-brown, dark on sides. Sternum black with median light and posterior median white mark. Coxae yellow-white. Legs with distal articles banded. Proximal ones yellow-white. Dorsum of abdomen with a black folium having jagged outline; lighter on sides of folium. Venter black with two paraxial light lines. Posterior median eyes 1.2 diameters of anterior medians; anterior laterals 0.5 diameter; posterior laterals 1.2 diameters of anterior medians. Anterior median eyes 1.5 diameters apart, 0.8 from laterals. Posterior median eyes 1.7 diameters apart, 1.8 from laterals. The abdomen is oval, dorsoventrally flattened. Total length, 3.6 mm. Carapace, 2.2 mm long, 2.0 mm wide. First femur, 2.6 mm; patella and tibia, 2.8 mm; metatarsus, 2.7 mm; tarsus, 1.2 mm. Second patella and tibia, 2.7 mm; third, 1.4 mm; fourth, 2.2 mm.

Diagnosis. The species is similar to *Argiope minuta* Karsch from Japan and *A. dietrichae*. The female differs by the very distinct abdominal pattern (Fig. 214) and the wider septum in the epigynum (Fig. 211). The male has a much heavier embolus and the median apophysis a shorter inside prong (Fig. 216).

Note. The epigynum of the holotype had one embolus tip stuck to it on the left side (Fig. 211) and had two on the right side (which were removed).

Natural History. The spiders were in webs at the mouth of sandstone caves on the walls of the Katherine Gorge, 10 to 100 m from Katherine River, in precipi-



Figures 205–210. *Argiope minuta* Karsch. 205–209. Female. 205. Epigynum, ventral. 206. Epigynum, posterior. 207. Epigynum, lateral. 208. Carapace and abdomen. 209. Sternum and abdomen. 210. Left male palpus, mesal.

Figures 211–216. *Argiope katherina* n. sp. 211–215. Female. 211. Epigynum, ventral. 212. Epigynum, posterior. 213. Epigynum, lateral. 214. Carapace and abdomen. 215. Sternum and abdomen. 216. Left male palpus, mesal.

Figures 217–221. *Argiope caledonia* n. sp., female. 217. Epigynum, ventral. 218. Epigynum, posterior. 219. Epigynum, lateral. 220. Carapace and abdomen. 221. Sternum and abdomen.

Scale lines. 0.1 mm, except Figures 208, 209, 214, 215, 220, 221, 1.0 mm.

tous terrain. Vegetation was sparse, *Pandanus* the dominant tree. The canopy was open, but the caves provided protection from sunlight; temperature was about 37°C, humidity 90% (the rainy season was just starting) (R. R. Jackson, correspondence).

Records. AUSTRALIA: *Northern Territory.* Pine Creek, 15 Oct. 1975, ♀ (P. Whelan, AMS).

Argiope caledonia new species

Figures 217–221; Map 4

Holotype. Female from 7 mi [11 km] SE of La Foa, New Caledonia, 16–22 April 1945 (C. L. Remington) in the American Museum of Natural History. The specific name is a noun in apposition after the type locality.

Description. Female from Mt. Koghi, Noumea, New Caledonia. Carapace dark brown, middle lighter, covered by white down. Sternum with a median light band and lighter spots on sides facing coxae (Fig. 221). Palpi yellow-white. Legs black with a light narrow ring around proximal part of tibiae and metatarsi. Dorsum of abdomen with black transverse bands (Fig. 220). Venter with a black band framed by two white longitudinal stripes (Fig. 221). Anterior lateral eyes 0.5 diameter of anterior medians. Posterior medians and posterior lateral eyes subequal to anterior medians. Anterior median eyes their diameter apart, 1.5 from laterals. Posterior median eyes 1.5 diameters apart, 2 from laterals. The abdomen is oval, truncate anteriorly, with small anterior lateral humps. Total length, 12.5 mm. Carapace, 5.2 mm long, 4.5 mm wide. First femur, 7.9 mm; patella and tibia, 8.6 mm; metatarsus, 8.0 mm; tarsus, 2.0 mm. Second patella and tibia, 8.5 mm; third, 4.3 mm; fourth, 7.6 mm.

Diagnosis. The abdomen differs from that of *A. keyserlingi* by lacking lobes on the sides of the posterior half of the abdomen (Figs. 220, 221). The depressions of the epigynum are much deeper than those of *A. keyserlingi*, and the lateral margin is curved convexly (Figs. 217, 218). In posterior view the posterior plate on each side disappears into a round opening; the opening is not bordered posteriorly (Fig. 218).

Distribution. New Caledonia, New Hebrides (Map 4).

Paratypes. NEW CALEDONIA: Mt. Koghi, 400 m, 12 March 1978, ♀ (E. I. Schlinger, EMB); 22 km E Bourall, 460–600 m, 6 March 1978, 2♀ (E. I. Schlinger, EMB).

Records. NEW CALEDONIA. 11 km SE La Foa, Feb.–April 1945, 2♀ (C. L. Remington, AMNH); Mt. Koghi, 400 to 500 m, Feb. 1973, ♀ (N. L. H. Krauss, AMNH); Noumea, Mt. Koghi, 5 July 1970, ♀ (T. W. Davies, CAS). NEW HEBRIDES: Anietyum, Aug. 1937, ♀ (L. Macmillan, AMNH); Espiritu Santo, 1943–1944, 3♀ (J. S. Haeger, AMNH); Erromanga Isl., March–April 1937, 2♀ (L. Macmillan, AMNH).

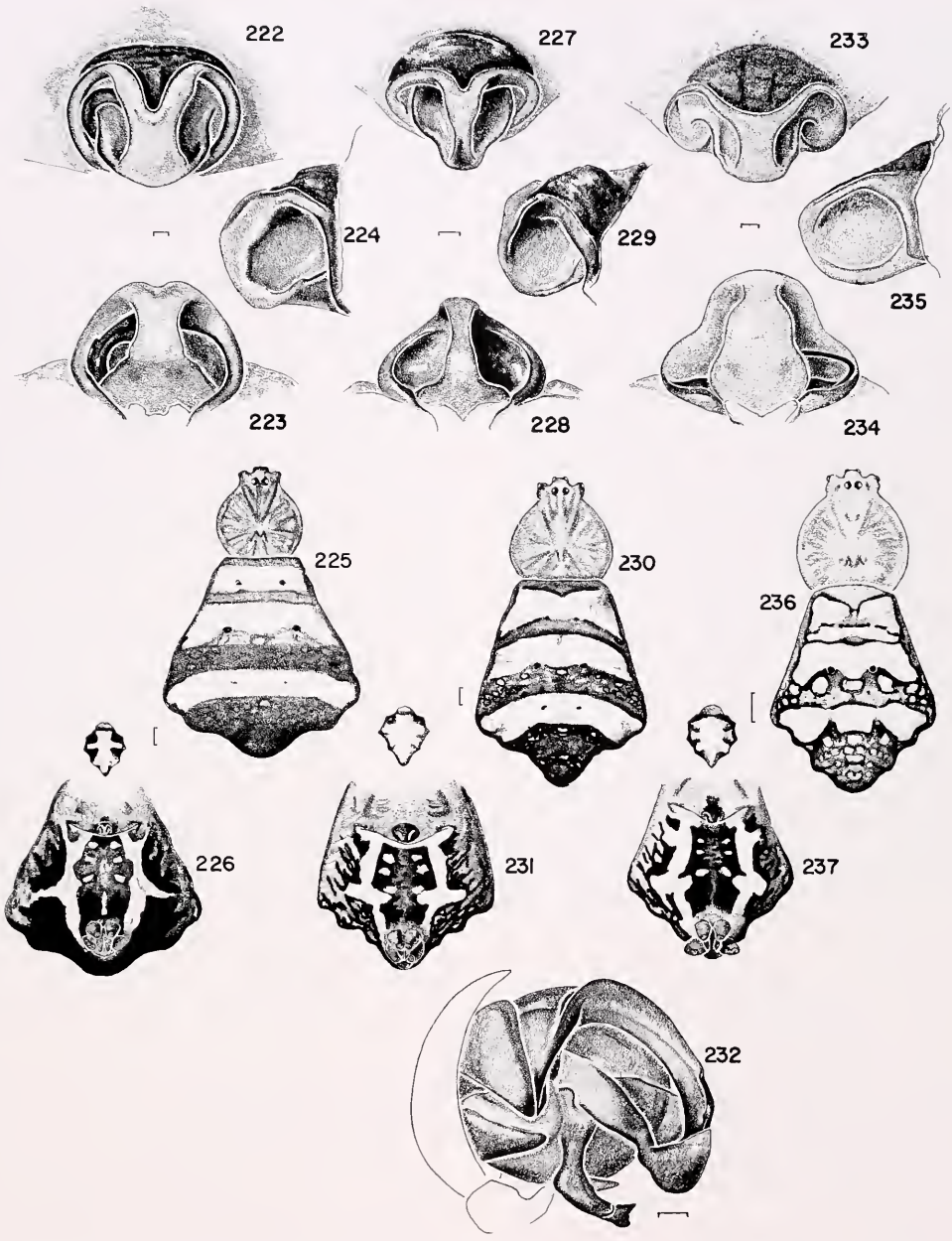
Argiope taprobanica Thorell

Figures 222–226; Map 5

Argiope taprobanica Thorell, 1887: 164. Female lectotype and juvenile paralectotype here designated from Taprobane [Island], Ceylon [Sri Lanka] in the Naturhistoriska Riksmuseet, Stockholm. Roewer, 1942: 739.

Note. According to Thorell (1887), the original specimens came from the O. P.—Cambridge collection. In the Cambridge collections in Oxford are two females from Ceylon marked *A. taprobanica*. But these are in fact *A. pulchella* and not the same species as the specimens in the Thorell collection in Stockholm. The female of the two Stockholm specimens is now labeled lectotype. There are no specimens with the name *A. taprobanica* in the Thorell collection in Genova, Italy.

Diagnosis. This species is probably close to *A. luzona* and perhaps *A. pulchella*, but the epigynum has a much wider septum and continues posteriorly into a wider posterior plate (Figs. 222, 223). The depression faces more ventrally; the rims



Figures 222–226. *Arigope taprobanica* Thorell, female. 222. Epigynum, ventral. 223. Epigynum, posterior. 224. Epigynum, lateral. 225. Carapace and abdomen. 226. Sternum and abdomen.

Figures 227–232. *Argiope luzona* (Walckenaer). 227–231. Female. 227. Epigynum, ventral. 228. Epigynum, posterior. 229. Epigynum, lateral. 230. Carapace and abdomen. 231. Sternum and abdomen. 232. Left male palpus, mesal.

Figures 233–237. *Argiope intricata* Simon, female. 233. Epigynum, ventral. 234. Epigynum, posterior. 235. Epigynum, lateral. 236. Carapace and abdomen. 237. Sternum and abdomen.

Scale lines. 0.1 mm, except Figures 225, 226, 230, 231, 236, 237, 1.0 mm.

curve posteriorly and are strongly sclerotized, forming the lateral margin of the depression. The rims appear polished (Figs. 222, 223). The embolus tip found in the epigynum (right depression, on left of Fig. 222) is a large bow resembling that of *A. luzona.*

Argiope luzona (Walckenaer)

Figures 227–232; Map 5

Epeira luzona Walckenaer, 1841: 109. Female specimens from Luzon, Philippine Islands, lost.

Argiope luzona:—Simon, 1877: 74. Roewer, 1942: 738. Bonnet, 1955: 690.

Note. Walckenaer described the broad black and silver transverse bands of the dorsum of the abdomen. The male and female have not been collected together, but are believed to belong together.

Diagnosis. The female of this large species has a pentagonal abdomen, the posterior lobed on the sides, and with broad black and silver transverse bands on the dorsum (Fig. 230). Unlike similar species and *A. intricata*, the septum anteriorly partly overlaps and bridges the rim, and the rim appears twisted (Fig. 227); the septum broadens posteriorly into a short posterior plate (Fig. 228). The continuation of the posterior plate dorsally fills the depression almost completely; the openings are anterior, lateral in the depression and only visible if the epigynum is viewed partly from the side.

The male differs from others by the tip of the conductor forming a basket containing the embolus tip, and by the relatively long median apophysis (Fig. 232).

Distribution. This species is only found on the northern islands of the Philippines (Map 5).

Records. PHILIPPINES: *Luzon.* Mt. Makiling [? Mt. Makelkelan], ♀♀ (Baker, SMF); Columba, Laguna Prov., 1 Sept. 1945, ♀ (S. G. Jewett, Jr., AMNH); Pasay City, Rizal Prov., ♀ (S. Wonechek, MCZ); Alabang, Rizal Prov., 20 Jan. 1957, ♀ (AMNH); Lucena, Tayabas Prov., 7 Oct. 1945, ♀ (B. Malkin, AMNH); Alabang, Rizal Prov., 20–30 July 1945, ♀ (W. Spector, AMNH); Los Baños, Laguna Prov., 16 Dec. 1945, ♂ (B. Malkin, AMNH). *Calicoan Island.* ♀ (F. F. Bibby, AMNH).

Argiope intricata Simon

Figures 233–237; Map 5

Argiope intricata Simon, 1877: 75. Original specimens from Malamoy [? Malamaui Isl.] and Basilan Isl., Philippines in the Muséum National d'Histoire Naturelle, Paris, lost. Roewer, 1942: 738. Bonnet, 1955: 687.

Note. Apparently at a later date Simon considered *A. intricata* and *A. luzona* the same, as there is a vial in the Muséum National d'Histoire Naturelle, Paris marked "*A. luzona* W. (=*intricata* E. S.) Manila det. Simon no. 9891" containing specimens of both.

Diagnosis. Argiope intricata is medium sized, smaller than *A. luzona*; the transverse bands on the dorsum of the abdomen have a jagged edge (Fig. 236). The opening of the epigynum, unlike that of *A. luzona*, can be seen surrounded by strongly curved lips on each side of the posterior plate in the middle of the depression (Fig. 236).

Distribution. Mindanao and Basilan Islands, Philippines (Map 5).

Records. PHILIPPINES: *Mindanao.* Mother Lode Mines, Surigao, 17 May 1950, ♀ (J. Bergseng, MCZ); Agusan River, Bunawan, 2♀ (Baker, AMNH).

Argiope pulchella Thorell

Figures 238–250; Map 5

Argiope pulchella Thorell, 1881: 74. Females reported from Celebes and near Tcibodas, Java [Cibodas, near Bogor]. Female syntypes [?] from "Mulmein" [Moulmein, Burma] in the Museo Civico di Storia Naturale, Genova, examined. Roewer, 1942: 738. Bonnet, 1955: 693.

Argiope undulata Thorell, 1887: 154. Female holotype from Schwego Mayo [Schwegu, near Bhamo], Burma in the Museo Civico di Storia Naturale, Genova, examined. Roewer, 1942: 739. NEW SYNONYMY.

Note. Bonnet (1955: 690) lists *undulata* as a synonym of *A. luzona*. This is a mistake. Figures 238–240 were made from the syntype of *A. pulchella*; Figures 241–243, 246, 247 from the syntypes of *A. undulata*; Figures 244, 245 from a specimen from Singapore and the male from Nepal (Figs. 248, 249).

Diagnosis. This species has an abdomen shape and coloration similar to *A. versicolor* but is much more variable in size, usually larger. Females vary in total length from 11.5 to 18.0 mm, carapace length, 4.0 to 6.1 mm; from Nepal, total length 10.7 mm, carapace length 3.9 mm. The epigynum has a smaller anterior bulge with a thicker V- or U-shaped rim (Figs. 244, 245) than *A. versicolor*, and the depressions face posterolaterally. In posterior view the epigynum is not as wide (Figs. 239, 242) as that of *A. versicolor*. Within the depression of mated females can be seen the torn-off duct from a male palpus (Fig. 239); usually only the very tip of the embolus (Fig. 250) becomes embedded in the opening (unlike *A. versicolor*, where a larger piece breaks off). Only rarely is a longer piece present; if it is, the pendant is as long as the tip, as in some Sumatra specimens. The internal genitalia of only a single female from Padang, Sumatra were examined and the seminal receptacles were found to be longer and narrower than those of *A. versicolor*.

The male palpus differs from that of *A. versicolor* by having the pendant longer than the embolus tip, having the duct near the tip of the embolus proximally approaching the margin of the embolus, and having the median apophysis longer in ventral view (Fig. 248).

Distribution. Thailand, India to Java (Map 5).

Records. CHINA: *Kiangsi Prov.* Hong San, 16 July 1936, ♀ (L. Gressitt, MCZ). THAILAND: Fang Hortic. Exp. Sta., Chieng Mai Prov., 19 Oct. 1981, ♀ (ZMK); Doi Inthanon Nat. Park, Chieng Mai Prov., 14 Oct. 1981, ♀ (ZMK); Chieng Mai, ♀ (L. Abra, AMS); Doi Suthep, Chieng Mai Prov., 800 m, 14 May 1958, ♂ (B. Degenbøl, ZMK); Choomporn [Chumphon], 15–20 Nov. 1957, ♀ (N. Meinkoth, MCZ). CAMBODIA: Stonkeve [Stŏeng Kêv], 1961, 2♀ (P. Skafte, ZMK). BURMA: Pegu, 3♀ (C. H. Carpenter, MCZ); Myitkyina, 1945, ♀ (D. N. Marks, AMNH); Mt. Popa, 4♀ (SMF). SINGAPORE: ♀ (H. N. Ridley, BMNH); Kalaw, 11 Nov. 1978, 2♀ (E. S. Ross, CAS). NEPAL: Tanhu Distr., Marsyandi, 400–500 m, Dumre-Turture, 7 April 1980, 3♀, 3♂ (J. Martens, Ausobsky, JMC); Kathmandu Valley, western part, 1300–1400 m, 17 Sept. 1964, ♀ (J. Martens, JMC); 1956–1958, ♀ (MCZ). INDIA: *Assam.* 13 km N of Silchar [? Sikar], 1–5 April 1969, ♀ (H. Hill, MCZ). "*North India.*" Kooloo Valley [Kulu], Himalaya, 1871, ♀ (M. Carlton, MCZ). *Dargiling* [Darjeeling]. ♀ (E. Reimoser, MCZ); ♀ (Gravely, NMW). *Bengal.* Calcutta, 1906–1907, house, ♀ (T. Barbour, MCZ). SRI LANKA: 2♀ (HCO), ♀ (NMW). INDONESIA: *Sumatra.* Deli [Labuhandeli], ♀ (BMNH), 24 April 1894, ♀ (W. Burchard, ZMH); Pulau Sertung [Verlaten Eiland], Dec. 1919, ♀ (Damm, AMNH); Medan, ♀ (E. Mjöberg, NRS); Kota Tajne [? Kotatinggi], ♀ (E. Mjöberg, NRS); Padang, ♀♀ (SMF); Fort de Kock [Bukittinggi], 900 m, 1924, ♀♀ (E. Jacobson, SMF).

Argiope versicolor (Doleschall)

Figures 3, 4, 251–262; Map 5

Epeira versicolor Doleschall, 1859: 31, pl. 9, fig. 10, ♀. Name given to illustration of specimens from Java. Two original Java specimens now labeled syntypes in the Rijksmuseum van Natuurlijke Historie, Leiden, examined. Roewer, 1942: 739. Bonnet, 1955: 698.

Argiope succincta L. Koch, 1871: 35. Female holotype from Borneo, lost; not in Zoologisches Museum, Universität Hamburg nor in British Museum.

Note. The type of *A. succincta* is lost. There is no doubt on the synonymy, since Koch described the diagnostic swollen anterior bulge of the epigynum; also, the

species is common in Borneo. Figures 254–258, 261, 262 were made from a female from Siberit, Sumatra; Figures 251–253 from Kepong, Selangor, Malaysia. The male Figures 259, 260 were made from a specimen from Kuala Lumpur, Malaysia.

Diagnosis. This species has the abdomen shape and epigynum similar to that of *A. pulchella*. All specimens are medium sized, none large. Total length of females, 8.6 to 12.0 mm; carapace length, 3.5 to 4.4 mm. *Argiope pulchella* may be much larger, but also sometimes is smaller. The epigynum in *A. versicolor* has a larger anterior bulge, the rim is thin and almost straight (Figs. 251, 254); in *A. pulchella* the thick rim describes a U-shape, and the depressions face posterolaterally. In posterior view the epigynum is wider in proportion (Figs. 252, 255) than that of *A. pulchella*. The broken-off parts of the palpal embolus in *A. versicolor* are large (Figs. 261, 262) and fit snugly inside the margins of the depression. They only become apparent as a separate structure if pushed in. Only the very tip is found in the epigynum of *A. pulchella*, and a torn-off duct hangs inside the depression. The internal genitalia of only one female from Panang, Malaysia were examined; the seminal receptacles were found wider and shorter than those of *A. pulchella*.

The embolus of the palpus lacks the dorsal kink of the *A. aetherea* group. An embolus tip from Java had the distal curved part above the duct (but not the pendant) more sclerotized and more distinct, similar to the tips found in *A. pulchella* epigyna. The palpus (Fig. 259) differs from that of *A. pulchella* in having the pendant shorter than the embolus, the duct almost through the middle of the embolus, and the median apophysis shorter in ventral view.

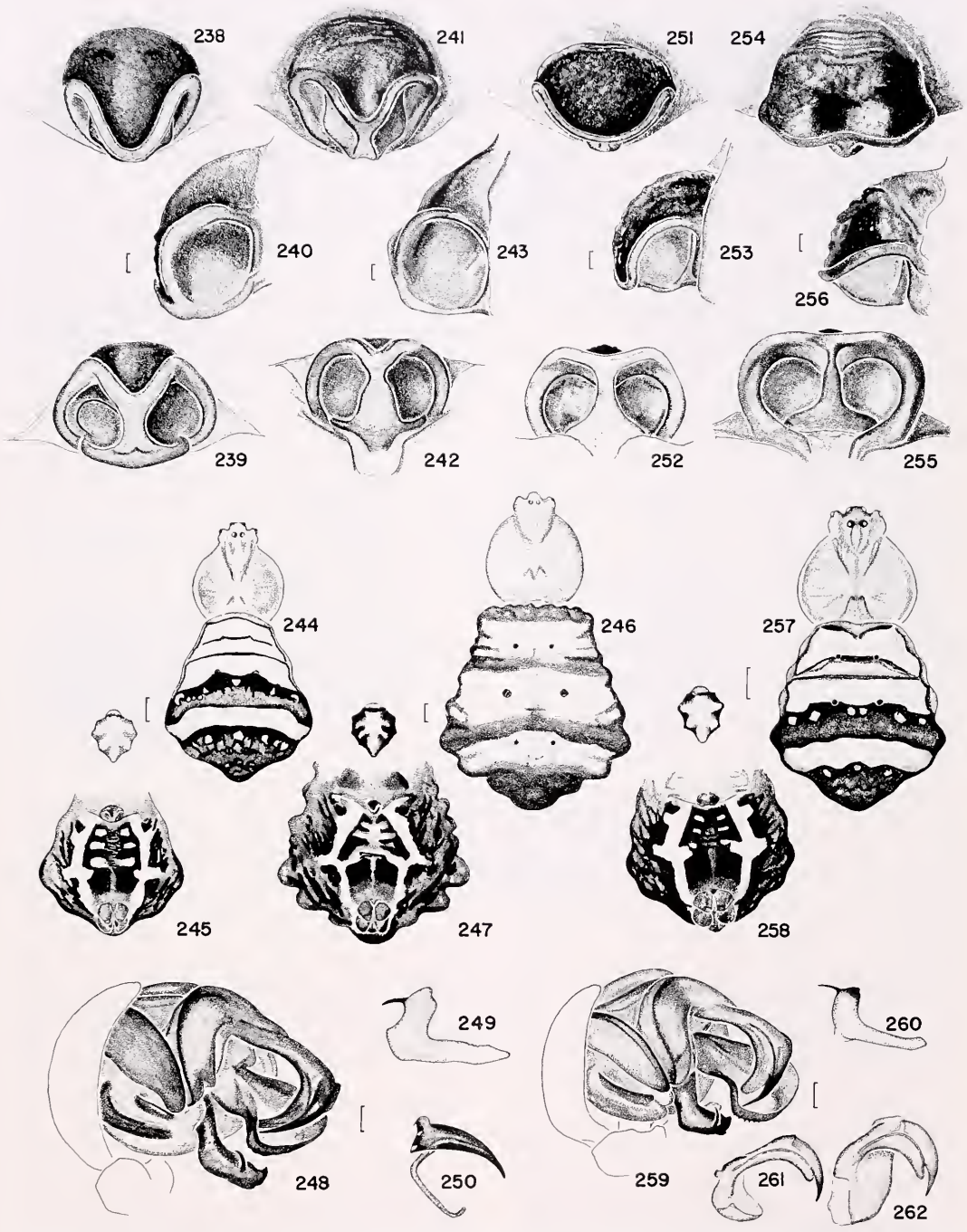
Distribution. Malaysia, Borneo, Sumatra, Java (Map 5).

Records. MALAYSIA: *Malay Peninsula.* Kedah Peak, 1000–1200 m, 28 April 1962 (E. S. Ross, CAS); 24 km N Kuala Lumpur, March 1949, ♀ (R. Traub, AMNH), bldgs., 30 April 1980, ♀♂ (J. A. Beatty, BC); Kepong, Sept. 1979, ♀♂ (P. Hillyard, BMNH); between Kuala Lumpur and Fraser's Hill, 14 Feb. 1974, ♀♂ (W. C. Sedgwick, MCZ); Fraser's Hill, 5 Feb. 1973, ♀, 8 April 1976, ♀ (W. C. Sedgwick, SC); Genting, 18–22 Aug. 1979, ♀, ♂ (F. & J. Murphy, MC). *Sarawak.* Ng. Ngungun, Sg. Ngemah, 24 Nov. 1974, ♂ (CNC); Sadong, Dec., ♀ (Smith, MCZ); Feb. 1976, ♀ (E. W. Classey, MC); Gunong, Mulu Natl. Park, May 1978, ♀ (F. Wanless, BMNH). *Sabah.* Gaya Island, 26 Jan. 1976, ♀ (E. W. Classey, MC); Porung [? Poring], 900 m, 19 Jan. 1976, ♀ (E. W. Classey, MC); 550 m, 22 Jan. 1976, ♀ (E. W. Classey, MC); Ulu Dusun, Sandakan, 29–31 Jan. 1976, 2♀ (E. W. Classey, MC). SINGAPORE: ♀ (H. N. Ridley, BMNH). INDONESIA: *Sumatra.* between Kotabaroe [Kotabaru] and Pajacombe [Pajakumbuh], June 1937, ♀ (C. T. Brues, MCZ); Fort de Kock [Bukittinggi], 1926, 5♀ (Jacobson, NMW), roadside farm, 14 July 1981, 7♀ (W. C. Sedgwick, SC); Harau Kloof, 23 April 1929, ♀ (S. A. R. Prince Léopold, IRSN); Panti, 26 April 1929, ♀ (S. A. R. Prince Léopold, IRSN); Pulau Sertung [Verlaten Eiland], Dec. 1919, ♀ (Damm, AMNH); Siberut [Isl.], 7 Feb. 1917, ♀ (O. Hagerup, ZMK); ♀♂ (Doria, NRS). *Java.* Buitenzorg [Bogor], March 1909, ♀ (O. Bryant, MCZ), ♀ (NMW); Tasikmalaja, in house, ♀ (Gornsten, NMW). *East Borneo*

→

Figures 238–250. *Argiope pulchella* Thorell. 238–247. Female. 238, 241. Epigynum, ventral. 239, 242. Epigynum, posterior. 240, 243. Epigynum, lateral. 238–240. (Moulmein, Burma). 241–243. (northeastern Burma). 244, 246. Carapace and abdomen. 245, 247. Sternum and abdomen. 244, 245. (Singapore). 246, 247. (northeastern Burma). 248. Left male palpus, mesal. 249. Median apophysis from "below." 250. Broken left embolus tip from an epigynum.

Figures 251–262. *Argiope versicolor* (Doleschall). 251–258. Female. 251, 254. Epigynum, ventral. 252, 255. Epigynum, pos-



terior. 253, 256. Epigynum, lateral. 251–253. (Salangor, Malaysia). 254–256. (Siberut, Sumatra). 257. Carapace and abdomen. 258. Sternum and abdomen. 259. Left male palpus, mesal. 260. Median apophysis from "below." 261, 262. Broken left embolus tip from an epigynum (at different angles).

Scale lines. 0.1 mm, except Figures 244–247, 257, 258, 1.0 mm.

[Kalimantan]. Long Navang [Long Nawan], ♀ (E. Mjöberg, NRS); Tewah, ♀ (Breitenstein, NMW).

Argiope modesta Thorell

Figures 263–270; Map 5

Argiope modesta Thorell, 1881: 75. Female holotype in poor condition from Kunang [? Kupang], Timor in the Museo Civico di Storia Naturale, Genova, examined. Roewer, 1942: 738. Bonnet, 1955: 691.

Argiope crenulata pictula Strand, 1911a: 203. Two female syntypes from Boeton [Butung], southeast Celebes in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Argiope appensa pictula:—Roewer, 1942: 740.

Argiope appensa:—Bonnet, 1955: 672 (in part).

Note. The type specimen of *A. modesta* is in poor condition (Figs. 263–265) and was first thought to belong to *A. appensa*.

The epigynum and abdomen (Figs. 266–270) were illustrated from the holotype of *A. pictula*.

Diagnosis. Like *Argiope appensa*, the rim of the epigynum appears broken, the anterior lateral part is a part of the anterior bulge without an intervening lip (Figs. 263, 266). Unlike *A. appensa*, the epigynum is ventrally pulled out (Figs. 265, 268). Also, the abdomen is lobed all around and has very distinct dorsal markings (Figs. 269, 270).

Variation. Two collections from Western Australia of specimens in poor condition seem to have just the posterior dorsal tip of the abdomen black, as in the related *A. aetherea*; the sides of the abdomen are lobed. A female from Taam Island, Australia has the abdomen banded as that of *A. rainbowi*.

Distribution. Borneo, Java, Celebes, Timor, Australia (Map 5).

Records. INDONESIA: *Java*, 2♀ (Seubort, SMF) *Lombok*. from hymenoptera nests, 29 May 1899, 2♀ (C. Auri-villius, NRS). *East Borneo*. Maratoea Island [Pulau Maratua], ♀ (E. Mjöberg, NRS). *Moluccas*. Key Duelah [Dula, Tual, Kep. Ewab], 1908, 6♀ (H. Merton, SMF). *Timor*. 5♀ (NHMW); Roti Isl. in grass, 23 July 1899, ♀ (C. Auri-villius, NRS).

Argiope appensa (Walckenaer)

Figures 271–278; Map 5

Epeira appensa Walckenaer, 1841: 111. Female without locality, lost.

Epeira (Argyopes) crenulata Doleschall, 1857: 414; 1859, pl. 3, fig. 7, ♀. Female specimens from Amboina [Ambon] in the Rijksmuseum van Natuurlijke Historie, Leiden, examined.

Argiope chrysorrhoea L. Koch, 1871: 38, pl. 3, fig. 5, ♀. Three female syntypes from the Pelew Inseln [Palau Isl.] in the Zoologisches Museum, Universität Hamburg, examined.

Argiope boetonica Strand, 1915: 215, pl. 16, fig. 53, ♂. Male holotype from Bau-Bau, Boeton, southeast Celebes in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Coganargiope (Micrargiope) reticulata Kishida, ?1931: 130; 1936: 22, figs. 6–11, ♀♂. ?Type specimens? NEW SYNONYMY.

Argiope crenulata:—Roewer, 1938: 33, fig. 23, ♀.

Argiope appensa:—Roewer, 1942: 740. Bonnet, 1955: 672. Chrysanthus, 1971: 10, figs. 4–8, ♀, ♂.

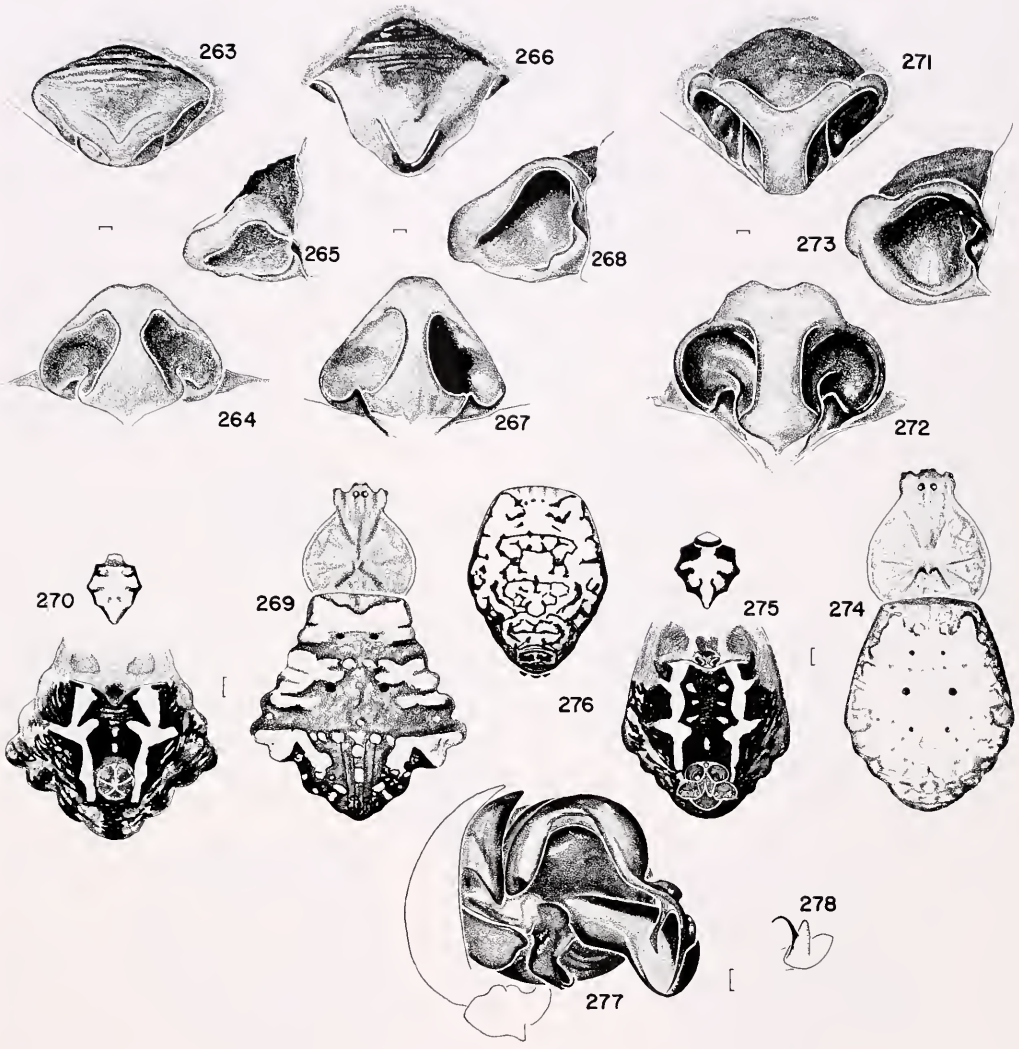
Argiope schoenigi Marapao, 1965: 45, pl. 1, ♀, ♂. Female holotype from Guadalupe, Cebu City, Philippines in the University San Carlos, Cebu City, not available. NEW SYNONYMY.

Notes. Walckenaer gave a good description of the unusual dorsal pattern. *Argiope boetonica* had been synonymized with *A. aetherea* by Chrysanthus (1971), an error.

The illustrations were made from specimens coming from Guam.

Diagnosis. This is a large *Argiope*. Females can be distinguished from other species by the reticulated pattern on the abdomen covering the dorsum completely in dark specimens, around the edge only in light ones (Figs. 274, 276). Unlike any other species (except *A. modesta*), the rim of the anterior bulge of the epigynum is broken anteriorly on each side; the median part is wide, the lateral narrow (Fig. 271).

The conductor of the male palpus (Fig. 277) is shorter than that of *A. aetherea*, its "upper" margin straight (compared to that of *A. picta* and other similar species). While the axis of the tip of the median apophysis is nearly parallel in position to the axis of the conductor in *A. aetherea* and *A. picta*, it is on angle, and the me-



Figures 263–270. *Argiope modesta* Thorell, female. 263, 266. Epigynum, ventral. 264, 267. Epigynum, posterior. 265, 268. Epigynum, lateral. 263–265. (Timor). 266–268. (Celebes). 269. Carapace and abdomen. 270. Sternum and abdomen.

Figures 271–278. *Argiope appensa* (Walckenaer). 271–276. Female. 271. Epigynum, ventral. 272. Epigynum, posterior. 273. Epigynum, lateral. 274. Carapace and abdomen. 275. Sternum and abdomen. 276. Abdomen, dorsal. 277. Left male palpus, mesal. 278. Median apophysis from "below."

Scale lines. 0.1 mm, except Figures 269, 270, 274–276, 1.0 mm.

dian apophysis is a shorter structure (Fig. 277), with the spur coming off the middle.

Distribution. Hawaii, Taiwan to New Guinea (Map 5).

Records. TAIWAN: Taipei, 11 Oct. 1955, ♀ (M. Walsh, AMNH). HAWAII: *Oahu.* Lualuale; Diamond Head Crater; Waipio; Ewa Plantation; Kunia Camp; Waialua, Mokuleia Beach, house and garden; Honolulu, McCully; Kaneohe. *Maui.*

Haiku; Seven Sacred Pools; 13 km S Hana. *Hawaii*. Hawaii Volcanoes National Park, Kamoamoa, bldgs.; Wahaula; trail to crater. MARSHALL ISLANDS: *Majuro Atoll*. grass, herbs, and shrubs, 22 March 1980, ♀♂ (J. A. Beatty, BC); 10 km E Laura, Long Isl., shrubs and trees, 24 March 1980, ♀ (J. A. Beatty, BC). MARIANA ISLANDS: *Guam*. bamboo-Pandanus forest, 4 April 1980, 2♀ (J. A. Beatty, BC); bldgs., 4 March 1973, ♀♂ (J. A. Beatty, BC); beach, 3 March 1973, ♀♂ (J. A. Beatty, BC); Mangilao, Nov. 1969, ♀♂ (E. Sabath, MCZ). CAROLINE ISLANDS: *Ponape Island*. Kolonia, bldgs., [numerous collections, BC, BPBM, MCZ), Uh Distr., shrubs, 27 March 1980, ♀ (J. A. Beatty, BC). *Ngajangel Isl., Kayangel Isl., Palau Isl.* (numerous collections, AMNH, BC, BPBM, MCZ, NMW). *Yap Isl.* (many collections, MCZ, BPBM). *Fais Isl.* 5 Dec. 1952, 2♀ (N. L. H. Krauss, BPBM). *Tobi Island*. trees in forest, 21 April 1973, ♀♂ (J. A. Beatty, E. Berry, BC); ♀ (SMF). *Sonsorol Island*. 13 Sept. 1952, ♀ (N. L. H. Krauss, BPBM); tropical forest, 6 April 1973, ♀ (J. W. Berry & E. Berry, BC). *Pulo Anna Isl*. 13 Sept. 1952, ♀ (N. L. H. Krauss, BPBM); 7 April 1973, ♀♂ (J. W. Berry, E. Berry, BC). PHILIPPINES: *Mindanao*. Anakan Lumber Co., Misamis Oriental, 12 May 1950, ♀ (J. Bergseng, FMC); Balingasag coastal road, 9–10 May 1950, ♀♂ (J. Bergseng, FMC); Mother Lode Mines, Surigao, 17 May 1950, ♂ (J. Bergseng, FMC). *Calicoan Island*. (AMNH). *Leboon Isl*. [Calicoan Isl.], 1945, ♀ (F. Bibby, AMNH). *Mactan Island*. Mactan, Dec. 1958, ♂ (N. L. H. Krauss, AMNH). INDONESIA: *Java*. ?Buitenzorg [Bogor], ♀ (SMD). *Celebes*. Menado, 13 Feb. 1929, ♀ (S. A. R. Prince Léopold, IRSN). *Molucca Islands*. *Morotai*: 10 July 1945, ♀ (B. Malkin, AMNH); *Ambon*: April 1908, ♀ (T. Barbour, MCZ), ♀♀ (Suyberbuyk, IRSN), 8♀ (Challenger Exped., BMNH); *Ternate*: 14 Feb. 1929, ♀ (S. A. R. Prince Léopold, IRSN), 1906–1907, ♀ (T. Barbour, MCZ). *Obi Island*: ♀ (T. Barbour, MCZ). *Bouron Island* [Buru Isl.]: Tifoe [Tifu], 1906–1907, ♀ (T. Barbour, MCZ). NEW GUINEA: ?Île Mansinam [Mausinam?], Manokwan, 8 March 1929, 3♀ (S. A. R. Prince Léopold, IRSN). *West Irian* [Djaya Pura]. Middleburg Isl., 3 July 1952, ♀ (RNHL); Purdy Islands, 19 June 1944, ♀ (C. B. Phillips); Archipel Manfield, "au N de Batanta," 1 March 1929, 3♀ (S. A. R. Prince Léopold, IRSN); Archipel Misool [Misoöl Isl.], Jef-bi, 26 Feb. 1929, 3♀ (S. A. R. Prince Léopold, IRSN). *Papua New Guinea*. Central Distr. Areana Estate, Galley Reach, 19–25 March 1966 (G. Bush, MCZ). Madang Distr. Fr. Wilhelmshafen [Madang], May 1909 (G. Duncker, ZMH). *Trobriand Islands*. Kiriwinia Isl., ♂ (W. B. Jones, AMNH).

Argiope brunnescentia Strand, new status

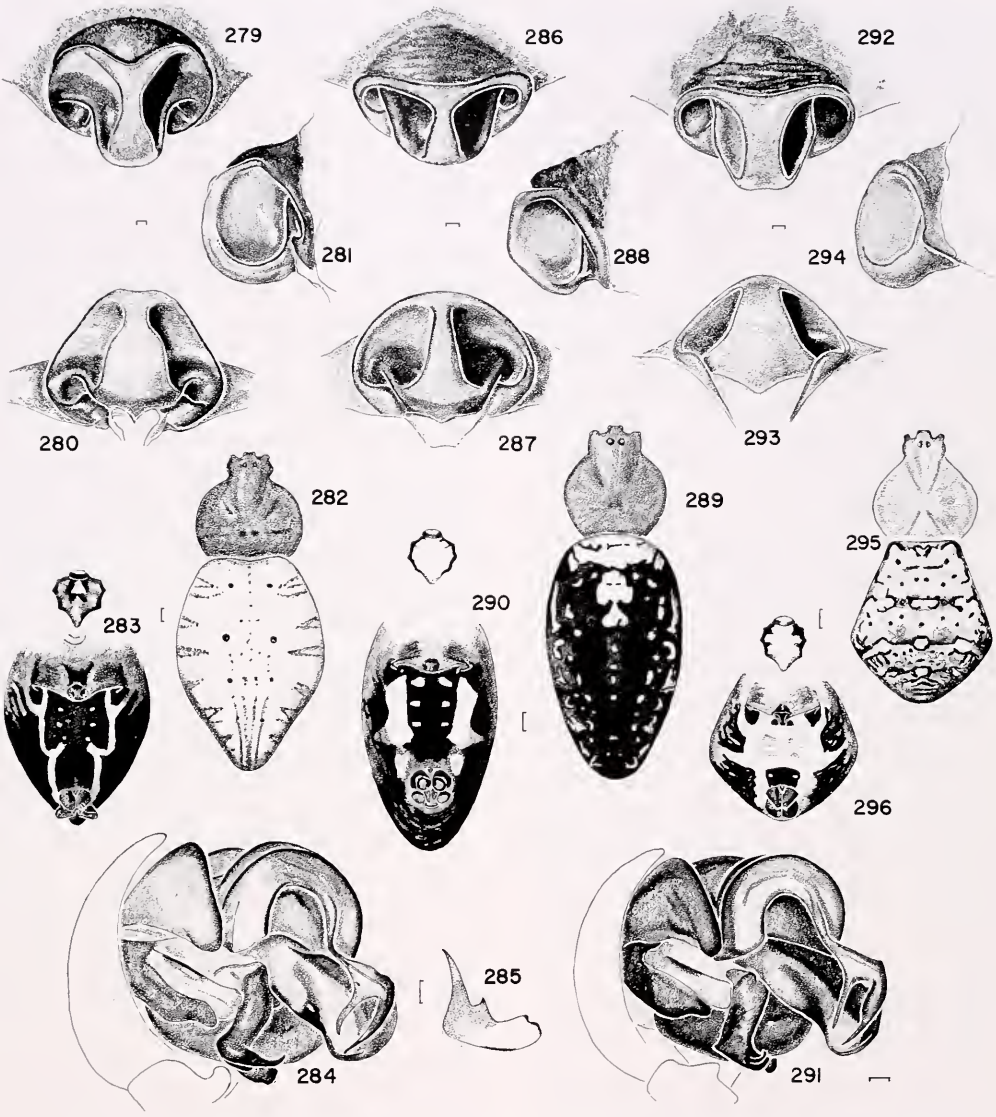
Figures 279–285; Map 5

Argiope avara brunnescentia Strand, 1911a: 203. Two female syntypes from Squally Insel [Tench Island, Bismarck Archipelago] in the Senckenberg Museum, Frankfurt, examined. Roewer, 1942: 740. Bonnet, 1955: 677.

Argiope squallica Strand, 1915: 216, pl. 16, fig. 54. Male holotype from Squally [Tench Island] in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Argiope avara:—Chrysanthus, 1971: 12 (in part), fig. 10, ♀. Misidentification; not *A. avara* Thorell [=*trifasciata*].

Note. The illustrations of the female were made from a syntype. The male type of *A. squallica* has only one palpus which is slightly expanded and therefore was not illustrated. The base of the embolus forms a much smaller semicircle than that of *A. aetherea*, *A. appensa*, and *A. picta*. It is like the palpus illustrated (Fig. 284) and like that of *A. bougainvilla*. However, the median apophysis is much more like that of *A. picta* (Fig. 315) than that illustrated by Figure 284. A second specimen labeled *A. squallica* by Strand from New Guinea is a male of *A. picta*. Only the syntype female illustrated (Figs. 279–283) had the ventral paraxial lines farther apart anteriorly than posteriorly. I have some doubt about every specimen examined, whether



Figures 279–285. *Argiope brunnescentia* Strand. 279–283. Female. 279. Epigynum, ventral. 280. Epigynum, posterior. 281. Epigynum, lateral. 282. Carapace and abdomen. 283. Sternum and abdomen. 284. Left male palpus, mesal. 285. Median apophysis from "below."

Figures 286–291. *Argiope bougainvilla* (Walckenaer). 286–290. Female. 286. Epigynum, ventral. 287. Epigynum, posterior. 288. Epigynum, lateral. 289. Carapace and abdomen. 290. Sternum and abdomen. 291. Left male palpus, mesal.

Figures 292–296. *Argiope pentagona* L. Koch, female. 292. Epigynum, ventral. 293. Epigynum, posterior. 294. Epigynum, lateral. 295. Carapace and abdomen. 296. Sternum and abdomen.

Scale lines. 0.1 mm, except Figures 282, 283, 289, 290, 295, 296, 1.0 mm.

it is conspecific with the type. A large series of females and males is needed to adequately diagnose this species.

Diagnosis. This species differs from *A. aetherea* by the laterally rounded shape of the abdomen, round in cross section, and by the dorsal abdominal markings (Fig. 282). The septum and posterior plate of the epigynum appear to be pulled in a posterior direction (Fig. 279).

The male from Oro Bay illustrated (Figs. 284, 285) may not belong to this species; it differs from others by having the spur of the median apophysis shaped like a large thorn (Figs. 284, 285) and having a pointed tooth near its base (Fig. 285).

Distribution. New Guinea, Bismarck Archipelago (Map 5).

Records. NEW GUINEA: *West Irian* [Djaya Pura]. Maffin Bay, Dec. 1944, ♀ (G. B. Sirotiak, AMNH): *Papua New Guinea.* Northern Distr. Oro Bay, ?1944, ♂ (B. Struck, AMNH). Madang Distr. Finisterre Mts., Naho River Valley, Budemu, 1270 m, 30 Oct.–23 Nov. 1964, ♀ (M. E. Bacchus, BMNH); Naho Riv. Vall., Moro, 1700 m, 30 Oct.–23 Nov. 1964, ♀ (M. E. Bacchus, BMNH). *Louisiade Archipelago.* Misima Isl., Mt. Sisa, 350 m, ♀ (L. Brass, AMNH). *Bismarck Archipelago.* Saint Matthias Group, south coast of Ebolin, Aturini Falls, Sept. 1908, ♀ (G. Duncker, ZMH).

Argiope bougainvilla (Walckenaer)

Figures 286–291; Map 5

Epeira bougainvilla Walckenaer, 1847: 473. Two specimens from the Solomon Islands, lost.

Argiope bougainvilla:—L. Koch, 1871: 42. Roewer, 1942: 741. Bonnet, 1955: 677.

Argiope vanicoriensis Simon, 1897: 272. Female holotype from Vanikora Island, Santa Cruz Islands, in the Muséum National d'Histoire Naturelle, examined. NEW SYNONYMY.

Argiope leopardina Pocock, 1898: 461, pl. 19, fig. 2, ♀. Two female syntypes from Solomon Islands, probably Shortland Island, in the British Museum, Natural History, examined. Roewer, 1942: 742. Bonnet, 1955: 687. NEW SYNONYMY.

Argiope leopardina clavifemur Strand, 1914: 216. Five syntypes from interior of Buka, Solomon Islands in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Argiope avara:—Chrysanthus, 1971: 12 (in part: figs. 9, 11, 12, ♀). Misidentification; *A. avara* = *A. trifasciata.*

Note. Walckenaer's description is enigmatic, but he describes the diagnostic, bright yellow dorsal patch on the abdomen and the smaller yellow dots behind, toward the sides. He must have had a light colored specimen, and dwelled on individual characteristics of his specimen. Pocock's description also has similar shortcomings, but his good illustrations and the presence of types removes all doubt. The illustrations (Figs. 286–290) were prepared from a syntype of *A. leopardina.*

Diagnosis. The elongate, oval abdomen of females bearing an anterior dorsal yellow patch (Fig. 289) readily distinguishes *A. bougainvilla* from all other species of *Argiope* except *A. trifasciata* from Kauai, Hawaii. The ventral abdominal marks (Fig. 290) may also be distinct, but are sometimes variable.

The shape of the epigynum separates this species from Hawaiian *A. trifasciata.*

The species differs from the related *A. appensa* by the abdomen shape, coloration, and by lacking the broken rim of the epigynum. The only male available had the distinct ventral markings of the female, and a smooth back of the tip of the embolus (Fig. 291). The axis of the base of the median apophysis is at a right angle to the axis of the conductor (Fig. 291).

Distribution. New Guinea?; Solomon Islands, Santa Cruz Islands (Map 5).

Records. PAPUA NEW GUINEA: *Madang Distr.* Finel Siar, near Friedrich Wilhelmshafen [Madang], 1906, 10♀ (error in locality?) (Schauinsland, SMF). SOLOMON ISLANDS: *Guadalcanal.* (many coll., AMNH). *Florida Island.* (AMNH). *New Georgia.* Munda (N. L. H. Krauss, AMNH). *Bougainville Isl.* (AMNH). *Russell Islands.* (R. B. Eads, AMNH; AMS). *Auki.* (W. M. Mann, MCZ). *Ugi.* (MCZ, AMS). *North Howla.* (AMS). *Isabel Isl.* ♀

(Albatross Exped., NMW). *Shortland Isl.* ♀ (Rechingen, NMW). SANTA CRUZ ISLANDS: Vanikora, ♀♀ (AMS).

Argiope pentagona L. Koch

Figures 292–296; Map 5

Argiope pentagona L. Koch, 1871: 39, pl. 3, fig. 6. Female holotype from Ovalau, Fiji in the Godeffroy Collection, Zoologisches Museum, Universität Hamburg, examined. Roewer, 1942: 742. Bonnet, 1955: 692.

Note. The dorsum of the abdomen of the type is white, the pattern washed out. The dorsal abdominal pattern in Figure 295 has been illustrated from a juvenile specimen having similar distinctive ventral markings (Fig. 296). The epigynum was illustrated from the type specimen.

Diagnosis. Like the epigynum of *A. bougainvilla*, the rim of the epigynum is almost straight (Fig. 292). It differs by having a wider septum (Fig. 292), a pentagonal-shaped abdomen (Figs. 295, 296), with a diagnostic square ventral white mark bearing eight arms (Fig. 296).

Records. FIJI ISLANDS: juv. (AMS); Mango Isl., 18 Sept. 1924, ♀ (E. H. Bryant, AMNH); Lami, Vit. Levu Isl., March 1955, ♀ (N. L. H. Krauss, BPBM).

Argiope aetherea (Walckenaer)

Figures 5, 6, 297–309; Map 5

Epeira aetherea Walckenaer, 1841: 112. Specimens from Port de Dorey, New Guinea [Dorei, Vogelkop Peninsula, West Irian], lost.

? *Argiope gorgonea* L. Koch, 1871: 35. Female specimen from Rockhampton, Queensland, L. Koch collection in the British Museum, Natural History, examined. The original description has the species coming from Boeroe [Buru Island, Moluccas].

Argiope regalis L. Koch, 1871: 36, pl. 3, fig. 4, ♀. Female holotype from Port Mackay, Queensland in the Godeffroy collection of the Zoologisches Museum, Universität Hamburg, examined.

Argiope variabilis Bradley, 1876: 141, pl. 1, fig. 3, ♀. Female lectotype and paralectotype here designated from Darnley Island, Torres Strait, in the Australian Museum, Sydney. examined.

Argiope lunata Bradley, 1876: 143, pl. 1, fig. 4, ♀. Female lectotype from Cocoanut Island, paralectotype from Sue Island, Torres Strait here designated in the Australian Museum, Sydney, examined. NEW SYNONYMY.

Argiope brownii O. P.-Cambridge, 1877: 284. Three female syntypes from Duke of York Island, New Britain in the Hope Entom. Collections, Oxford Univ., examined. NEW SYNONYMY.

Argiope keyserlingi:—Bösenberg and Strand, 1906: 199, pl. 11, fig. 230, ♀. Misidentification; not *A. keyserlingi* Karsch.

Argiope verecunda Thorell, 1878: 35. Female holotype in very poor condition from Amboina [Ambon], Moluccas in the Museo Civico di Storia Naturale, Genova, examined. NEW SYNONYMY.

Argiope aetherea annulipes Thorell, 1881: 68. Female holotype from Yule Isl. [nr. Port Moresby, New Guinea] in the Museo Civico di Storia Naturale, Genova, examined. According to Thorell the specimen came from "New Guinea."

Argiope aetherea deusta Thorell, 1881: 68. Two female syntypes in poor condition from Fly River, New Guinea in the Museo Civico di Storia Naturale, Genova, examined. According to Thorell (1881) the specimens came from Yule Island [nr. Port Moresby, New Guinea].

Argiope maerens, Kulczynski, 1911: 473, pl. 20, fig. 45, ♀. Female holotype from New Guinea in the Polish Academy of Sciences, Warsaw, examined. NEW SYNONYMY.

Argiope avara ocelligera Strand, 1911a: 203. Two female syntypes from Keule Insel [Koil], New Guinea in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

? *Argiope avara tristipes* Strand, 1911a, 77: 203. Female type from Squally Island [Tench Island, Bismarck Archipelago], lost. DOUBTFUL NEW SYNONYMY.

Argiope avara angulicosta Strand, 1911a: 203. A female holotype from Keule Insel [Koil], New Guinea in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Argiope friedericii Strand, 1911a: 204; 1915: 214, pl. 17, fig. 62, ♀. Female holotype, two paratypes from Eitape, German New Guinea [Aitape, Papua New Guinea] in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Argiope wolfi Strand, 1911a: 204; 1915: 212, pl. 16, fig. 55, ♀. Three female syntypes from Auer near Neu Mecklenburg [New Ireland] in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Argiope aetherea tangana Strand, 1911a: 204; 1915: 211. Juvenile female from Tanga Islands near Neu Mecklenburg [New Ireland] in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Argiope aetherea melanopalpis Strand, 1911a: 204. One juvenile, two female syntypes from Lamassa [Lamassong], Neu Mecklenburg [New Ireland] in the Senckenberg Museum, Frankfurt, examined. Strand, 1914: 211. NEW SYNONYMY.

Argiope udjirica Strand, 1911b: 142, pl. 5, fig. 43, ♀.

Female holotype from Aru Island in the Senckenberg Museum, Frankfurt, examined. Roewer, 1938: 33, fig. 22, ♀. Roewer, 1942: 743. NEW SYNONYMY.

Argiope aetherea keyensis Strand, 1911b: 145. Female holotype from Gross Key, Elat [Great Key, Banda Sea] in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Argiope lihirica Strand, 1913: 116; 1915: 215, pl. 13, fig. 14, pl. 16, fig. 52, ♀. Female holotype from Lihir near Neu Mecklenburg [New Ireland] in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Argiope wogeonicola Strand, 1913: 116; 1914: 213, pl. 16, fig. 56, pl. 17, fig. 58, ♀. Female holotype from Wogeo, Schouten Isl. [Vokeo Isl., Papua New Guinea] in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Argiope novaepommeraniae Strand, 1915: 212, pl. 16, fig. 51, ♀. Female holotype from Toma, Neu Pommern [New Britain] in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Gea rotunda Hogg, 1915: 244, fig. 24, ♂. Male holotype from Dutch New Guinea [West Irian] in the British Museum, Natural History, examined. NEW SYNONYMY.

Chaetargiope (*Neargiope*) *regalis*:—Kishida, 1936: 21.

Argiope aetherea:—Chrysanthus, 1958: 237, figs. 7–12, 24, ♀, ♂. M. H. Robinson, Lubin, and B. Robinson, 1974: 128. M. H. Robinson and B. Robinson, 1980: 10, 50, 79–83, 85, figs. 34–36 (photo).

Notes. Karsch wrote (1878: 788) that what Keyserling (1865) considered *A. aetherea* from New South Wales, Australia is probably a misidentification. Karsch continued to say that he had specimens from Japan that better fitted Walckenaer's description, but they had different epigyna from the specimens from Australia. He went on to say that these specimens from Japan may not be the right *aetherea*, since no specimens of the real *aetherea* from Australia were available for comparison. He then proceeded to give the name *A. keyserlingi* to Keyserling's specimens from Sydney, Australia and started a chain of confusion. The Asian species is here called *A. boesenbergi*, and the southern Australian species *A. keyserlingi*.

The type of *A. verecunda* Thorell is in poor physical condition, and the pattern of the abdomen has disappeared (the color had been lost when Thorell described it). The yellow sternum and shape of the epigynum indicate that it is *A. aetherea*.

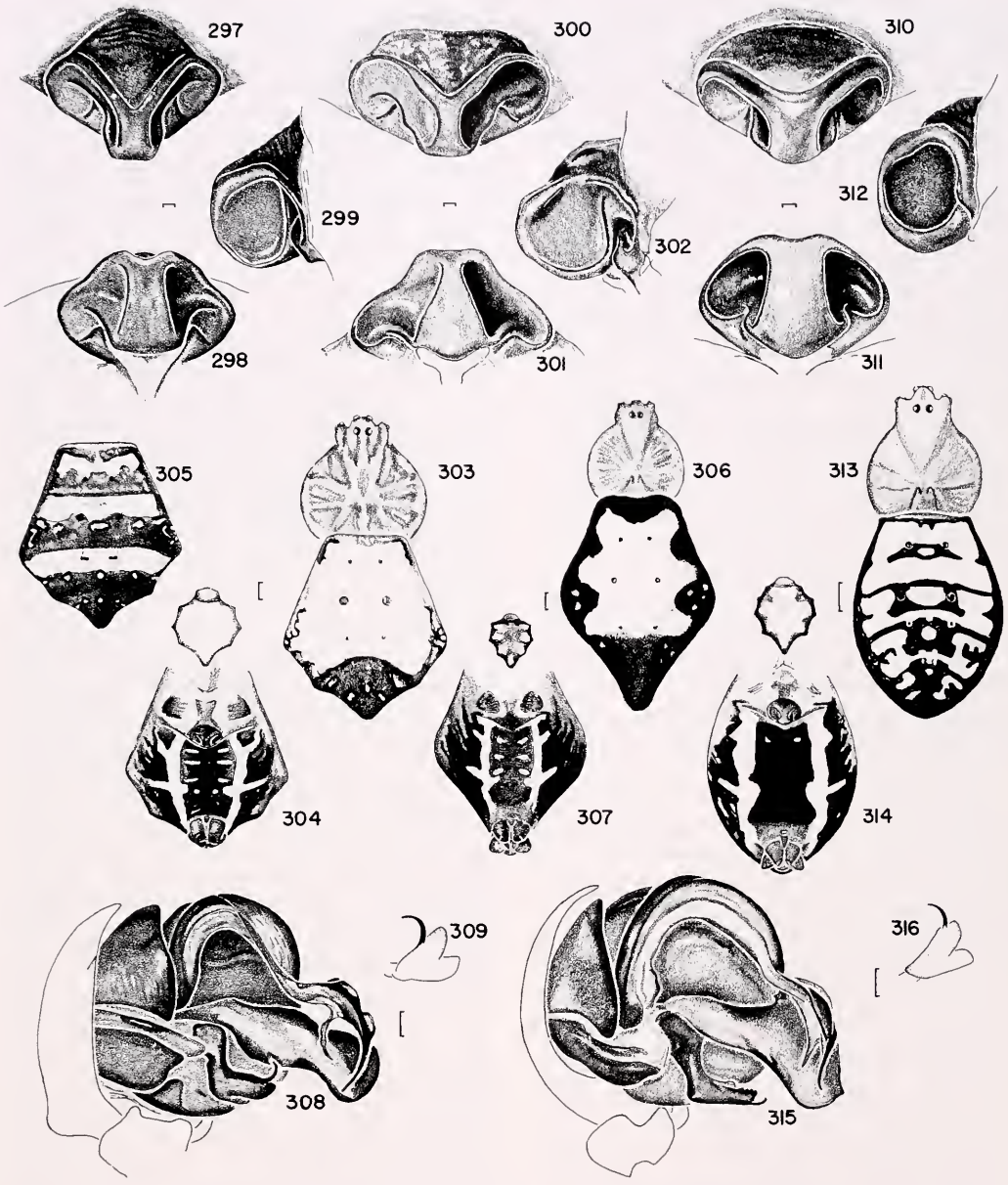
Roewer (1942) has synonymized *A. gorgonea* with *A. picta*. This may be an error. The pattern of the specimen available and named by Karsch resembles that of *A. aetherea* except for the sternum, which is like that of *A. picta*. The epigynum is perhaps closer to *A. picta*. The vial label has the specimen coming from Rockhampton, Queensland; the original description is of a specimen from Boeroe [Buru Island, Moluccas].

The specimens of *A. avara ocelligera* Strand and *A. avara angulicosta* Strand are melanistic (the dorsum of the abdomen is all black). All the other types examined and newly synonymized had genitalia and abdominal pattern within the variation of *A. aetherea*.

Diagnosis. Argiope aetherea differs from other similar species by the pentagonal shape of the abdomen (Fig. 303); from *A. picta* also by the dorsal abdominal markings (Figs. 303–305) and the anterior lip of the opening in the depression of the epigynum (Figs. 297, 300) which flares to each side (unlike *A. picta*); and by the yellow-to-orange color of the sternum (Fig. 304) (compared to the white markings on the venter). The anterior white branch of the paraxial white line on the venter of the abdomen is long in *A. aetherea*, short in *A. picta*.

The palpus of the male differs from that of *A. picta* in several ways: in lacking an "upper" lobe on the conductor behind the embolus; in the pendant of the embolus occurring at a greater distance from the tip; and in the orientation of the spur toward the embolus on the "upper" surface of the median apophysis (Figs. 308, 309) (on the "lower" edge of the tip in *A. picta*).

Variation. The species of this group, close to *A. aetherea*, hardly differ in genitalia. It is clear, however, that the sympatric *A. picta* is distinct. But are *A. truk* and *A. brunnescentia* forms of *A. aetherea*? The Solomon Island specimens (Figs.



Figures 297–309. *Argiope aetherea* (Walckenaer). 297–307. Female. 297, 300. Epigynum, ventral. 298, 301. Epigynum, posterior. 299, 302. Epigynum, lateral. 297–299. (Lae, Papua New Guinea). 300–302. (New Georgia, Solomon Islds.). 303, 306. Carapace and abdomen. 304, 307. Sternum and abdomen. 305. Abdomen, dorsal. 303–304. (Lae, Papua New Guinea). 305. (Buso, Papua New Guinea). 306–307. (New Georgia, Solomon Islds.). 308. Left male palpus, mesal. 309. Median apophysis from "below."

Figures 310–316. *Argiope picta* L. Koch. 310–314. Female. 310. Epigynum, ventral. 311. Epigynum, posterior. 312. Epigynum, lateral. 313. Carapace and abdomen. 314. Sternum and abdomen. 315. Left male palpus, mesal. 316. Median apophysis from "below."

Scale lines. 0.1 mm, except Figures 303–307, 313–314, 1.0 mm.

300–302, 306, 307) for a while were believed to be distinct. But other than having the sternum infused with some black pigment from the sides (also in some Australian specimens) and perhaps having slightly different proportions of the abdomen (Fig. 306), no consistent differences could be found.

The dorsum of the abdomen may have several wide transverse black bands, as in *A. reinwardti* (Fig. 305); may be completely white in preserved specimens; or bright yellow in living ones, always with a black posterior mark (Fig. 303). Australian specimens have similar variation in color of the abdomen but have the sternum a less bright yellow. There are also differences in the epigynum, especially in the configuration of the median and posterior lips of the openings; the rim is also thinner (Figs. 297, 300).

The female illustrated (Figs. 297–299, 303, 304) came from Lae, the banded abdomen from Buso (Fig. 303), and the male from Madang (Fig. 308), all Papua New Guinea. Figures 300–302, 306, 307 were made from a specimen from New Georgia Island, Solomon Islands.

Natural History. Argiope aetherea is common in gardens and disturbed coastal forests in Papua New Guinea; it is not found inland at Wau (M. H. Robinson, Lubin, and B. Robinson, 1974, and my own observations). Courtship and mating behavior are described in M. H. Robinson and B. Robinson, 1980.

Large New Guinea collections obtained between 1880 and 1914 and housed in the Berlin Museum have only a few specimens of *A. aetherea*. It must have been much less common along the coast at that time than more recently.

Distribution. Ambon, New Guinea to Solomon Islands, New Hebrides, northern Australia (Map 5).

Records. INDONESIA: *Kepulauan Aru.* Pulai Workai, Gomogomo, 2♀ (SMF); Poloe Enoe, ♀♀ (S. A. R. Prince Léopold Exped., IRSN). NEW GUINEA: *West Irian* [Djaya Pura]. Geelvink Baai, Legare; Merauke, 2♀ (SMF), 1956–1957, 3♀ (Br. Momelphus, IRSN); Menapi, Cape Vogel Peninsula. *Papua New Guinea.* Morobe Distr. Buso River; Finschhafen. Western Distr. Lake Daviumbu, Middle Fly Riv. Northern Distr. Oro Bay; Peria Cr., Kwagira Riv. [Kwagila Riv.]; Buna. Central Distr. St. Joseph's Riv. [Angabunga]. Madang Distr. Stephansort, Astrolabe Bay. Milne Bay Distr. Modewa Bay, W of Samarai. *D'Entrecasteaux Islands.* Goodenough Isl.; Normanby Isl. *Louisiade Archipelago.* Rossel Isl.; Mt. Sisa, Misima Isl.; Teste Isl., ♀ (AMS). *Trobriand Islands.* Hall Sound; Woodlark Isl.; Kiriwina Isl. *Admiralty Islands. Chagos Archipelago.* Sudest Island, Iamelele. *Bismarck Archipelago.* Maroon Isl., ♀ (AMS). *New Britain.* Matupi; Ralum, Simpsonhafen [Rabaul] (ZMB). *Solomon Islands.* New Georgia Island: Segi Point, Feb.–May 1944, 2♀, 5 juv. (C. O. Berg, MCZ, AMS); Bio, 1916, ♀ (W. M. Mann, MCZ). Guadalcanal: (many collections, AMNH, CAS). Russell Islands: (AMNH, AMS). Ysabel Island [Santa Isabel]: ♀ (N. S. Heffernan, AMS). Rendova: Hopongo, Nov. 1972, ♀ (N. L. H. Krauss, AMNH). *Santa Cruz Islands.* Reef Isl., 21 July 1926, ♀ (E. Troughton, AMS); Trevanton Isl., July 1926, ♀ (E. Troughton, AMS); Vanikoro, 9 Aug. 1926, ♀ (E. Troughton, AMS). *Torres Strait.* Cocoanut Isl., ♀ (H. H. B. Bradley, AMS); Sue Isl., 2♀ (H. H. B. Bradley, AMS). NEW HEBRIDES: Nov.–Dec. 1943, ♀, 2♂ (W. R. Enns, AMNH). *Espirito Santo.* Oct.–Dec. 1943, 3♀, May 1944, 12♀ (G. Banner, AMNH); 1943–1944, 3♀ (J. S. Haeger, AMNH). *Efate.* Jan.–Feb. 1973, 2♀ (N. L. H. Krauss, AMNH). *Erromagna Isl.* March–April 1973, 2♀ (L. Macmillan, AMNH). AUSTRALIA: *Northern Territory.* Barnard Isl.; Howard Springs Reserve [SE of Darwin]; Darwin; W. Alligator Mouth. *Queensland.* 27 km E Mount Garnet; Bellenden Ker; Palm Park [SE Byfield]; Rockhampton; Iron Range; Cairns; Wenlock; Portland Roads; Ravenshoe; Townsville; Fitzroy Isl.; Rainbow Beach; Whitsunday Isl. Gp.; Edmonton; Hayman

Isl.; Almaden; Helenvale, S of Cooktown; Mt. Dryander, N of Proserpine. *Great Barrier Reef.* Penrith Island, 2 Aug. 1969, ♀ (H. Heatwole, AMS); Lizard Isl., 25 Oct. 1967, ♀ (H. Heatwole, AMS). *Western Australia.* Derby Narth, ♀ (AMS); Sir Graham Moore Isl., 16–26 Feb. 1945, ♀ (B. Malkin, AMNH); Anjo Peninsula, 14–15 Feb. 1945, ♀ (B. Malkin, AMNH).

Argiope picta L. Koch

Figures 7, 8, 310–316; Map 5

Argiope picta L. Koch, 1871: 33, pl. 3, fig. 3, ♀. Two female syntypes from Port Mackay, 19°S, near Townsville, Queensland, Australia in the Godeffroy collection, Zoologisches Museum, Universität Hamburg, examined. Roewer, 1942: 743. Bonnet, 1955: 692. Chrysanthus, 1958: 237, figs. 1–6, 21, 23, ♀, ♂; 1971: 14. B. C. Robinson and M. H. Robinson, 1974: 145, pl. 2 (photo). M. H. Robinson, Lubin, and B. Robinson, 1974: 118. M. H. Robinson and B. Robinson, 1980: 10, 46, 50, 55, 71, 73–81, 85, 88–89, figs. 30–33.

Argiope principalis L. Koch, 1872: 207, pl. 18, fig. 5, ♀. Female holotype from Bowen [Fort Denisson], Queensland in the British Museum, Natural History, examined. Roewer, 1942: 743.

Argiope lugubris L. Koch, 1872: 209, pl. 18, figs. 6, 7. Male and juvenile female syntypes from Bowen [Fort Denisson], Queensland in the British Museum, Natural History, examined. Roewer, 1942: 742. Bonnet, 1955: 690. NEW SYNONYMY.

Argiope picta faorensis Thorell, 1881: 65. Female type from Pheo Faor, New Guinea in the Naturhistoriska Riksmuseet, Stockholm, examined.

?*Gea dubiosa* Strand, 1911b: 146, pl. 4, fig. 11, juv. Parts of juvenile holotype in very poor condition from between Gueramaguarin and Eresin, Teranga [Aru Island] in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Chaetargiope picta:—Kishida, 1936: 20.

Notes. Gea dubiosa is an early instar *Argiope* or *Gea* with a white spot in the middle posteriorly on the abdomen. It belongs to this species or perhaps to *Gea spinipes*, but it appears to come from a locality outside the range of *Gea spinipes*.

The specimens illustrated (Figs. 311–313) came from teak forest, Madang; Figure 310 from Wau, Papua New Guinea. Mascord (1978: 6) presents color photograph with the name *A. principalis*.

Diagnosis. This species can be confused with *A. aetherea*. Females differ by the distinct dorsal markings and the shield-shaped abdomen (Fig. 313). The sternum is not as bright orange as that of *A. aetherea*.

The epigynum is very similar to that of *A. aetherea* and quite difficult to separate consistently. Within the depression, the lateral edges of the posterior plate which form the anterior lip of the opening end closer to the midline (Fig. 310), and the rim is thicker than in *A. aetherea*.

The male differs from that of *A. aetherea* in having the spur at the very tip of the median apophysis in mesal view (Figs. 315, 316); in *A. aetherea* the spur is on the "upper" margin in mesal view.

Natural History. Argiope picta is found in shaded forest edge in the Wau area of Papua New Guinea. The web may have an X-shaped stabilimentum with the branches crossing the hub; most often the stabilimentum is absent (B. C. Robinson and M. H. Robinson, 1974). Females are common throughout the year (M. H. Robinson, Lubin, and B. Robinson, 1974). Courtship and mating behavior is described in M. H. Robinson and B. Robinson, 1980.

New Guinea collections obtained between 1880's and 1914 in the Berlin Museum are mostly *A. picta*, with very few *A. aetherea*. It must have been much more common at that time than it now is. The specimens had been misidentified as *A. aetherea* by F. Dahl.

Distribution. Moluccas, New Guinea to northern Australia and New Hebrides (Map 5).

Records. MOLUCCAS: *Morotai.* 6 Jan. 1945, ♀ (E. Reimschlisel, AMNH); 1944, ♂ (G. Banner, AMNH). *Ceram.* Wahaari [? Wahai], 1906–1907, ♀ (T. Barbour, MCZ). *Halmahera.* Djailolo, 16 Feb. 1929, ♀ doubtful det. (S. A. R. Prince Léopold, IRSN). *Aru.* Soengi Manoembaai, 26 March 1929, ♀♀ (S. A. R. Prince Léopold, IRSN). NEW GUINEA: *West Irian* [Djaya Pura]. Hollandia [Djaya]; Merauke, 1956–1957, ♀, ♂ (Br. Monulf, MCZ); Fakfak, 6

July 1939, ♀ (R. G. Wind, MCZ); Maffin Bay, Sept. 1944, (E. S. Ross, CAS); Dec. 1944, ♂ (G. B. Sirotiak, Tana [? Tanamerah] Aug. 1910, ♀ (Moszkowski, ZMB); Teba, May 1910, ♀ (Moszkowski, ZMB). Seroel, Japen 6 March 1929, ♂ (S. A. R. Prince Léopold, IRSN). Mindiptana, 1959, ♂ (Br. Monulf, IRSN). *Papua New Guinea*. Many collections. *New Britain*. Herbertshöhe [? Kokopo], March 1903, ♀ (Dempwolff, ZMB); Ralum [Gazelle Penins.], June 1896, ♀ (F. Dahl, ZMB). SOLOMON ISLANDS: *Isabel Island*. 1 June 1925, ♀ (N. S. Heffernan, AMS); 3♀ (Albatross Exped., NMW). *Russell Islands*. Dec. 1944, ♀♂ (R. B. Eads, AMNH). *New Georgia*. Ugi, ♀ (AMS). Malaita, Auki, Dec. 1972, ♀ (N. L. H. Krauss, AMNH). Gizo, Nov. 1972, ♀ (N. L. H. Krauss, AMNH). *Guadalcanal*. (several collections, AMNH, CAS, MCZ). *Santa Cruz*. ♀ (W. M. Mann, MCZ); Pamira, ♀ (W. M. Mann, MCZ); Trevanion Isl. off Santa Cruz Isl., 10:30 S, 166:00 E, ♀ (Troughton and Livingston, AMS). AUSTRALIA: *Queensland*. Townsville; Cooktown; Edmonton; Iron Range; Mossman Riv. Gorge; Telegraph Crossing; Koak; Cairns; Redlynch; Kuranda; 10 km W Gordonvale; 5 km S Cardwell; Aloomba; Innisfail; Fitzroy Island; Edmonton; Bellenden Ker. *Northern Territory*. Howard Springs Reserve, 24 km SE Darwin, shrubs, 23 June 1923, ♀ (J. A. Beatty, BC); Darwin, March 1945, ♀ (B. Malkin, AMNH); E Alligator Riv., May 1979, ♂♂ (P. Davie, QMB). *Great Barrier Reef*. Lizard Isl., 27 Sept. 1967, ♂ (AMS); 8 km W Ravenshoe, 780 m, 6 Nov. 1962 (E. S. Ross, CAS); Thursday Isl., ♂ (AMS). NEW HEBRIDES: Aore Island, April 1944, ♀ (W. L. Nutting, MCZ).

Argiope radon new species

Figures 317–323; Map 5

Argiope sp. "N.T. riverine," M. H. Robinson and B. Robinson, 1980: 10, 50, 85–88, figs. 39–41, ♀ (web photo).

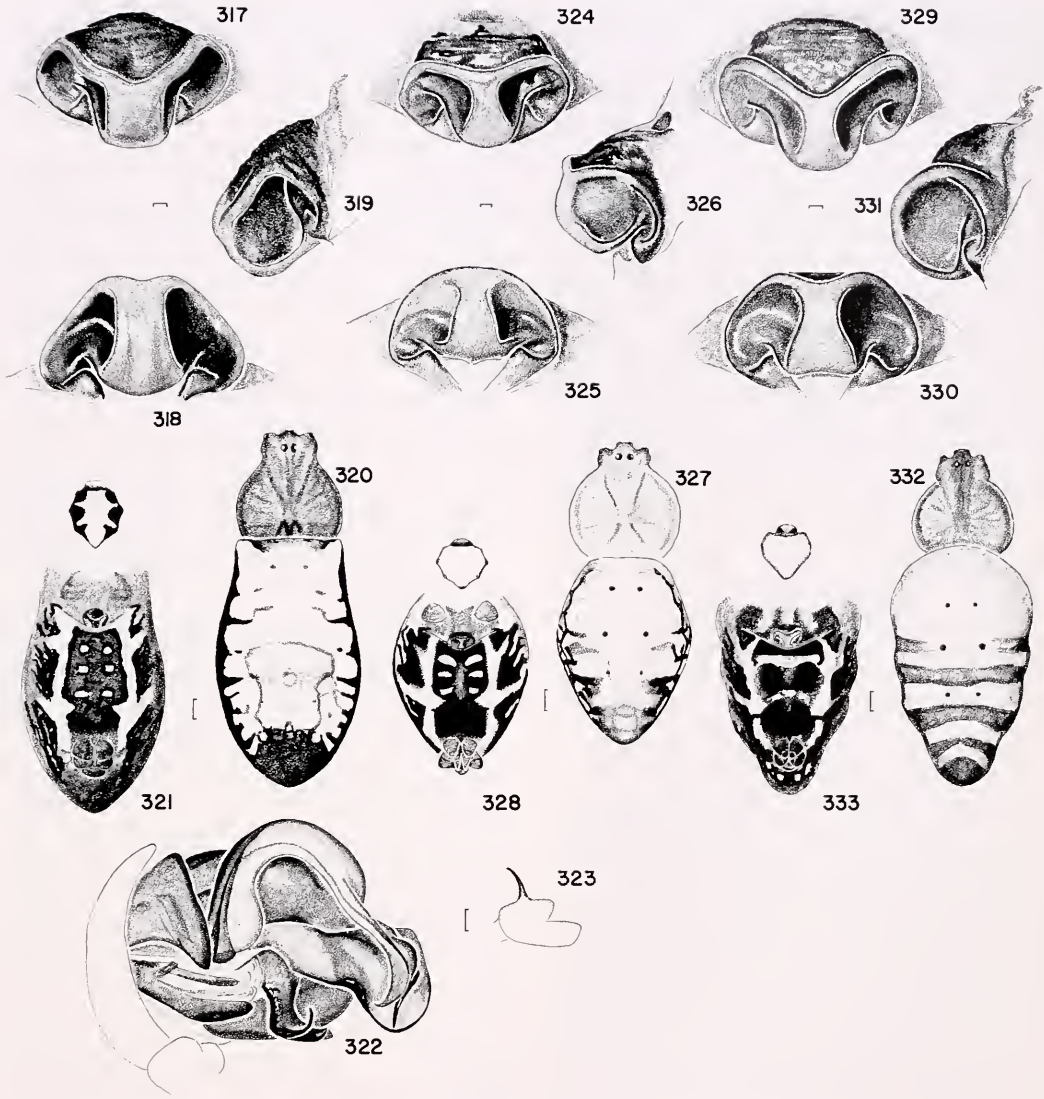
Holotype. Female; two males, one female, two juvenile paratypes from Radon Creek [12.45°S, 132.53°E], rainforest, Northern Territory, Australia, Nov. 1979, in the Queensland Museum, Brisbane, No. S906. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace streaked dark brown, covered by white down. Sternum black, middle white (Fig. 321). Dorsum of abdomen mottled white, covered by white setae, framed by black, and posterior tip black (Fig. 320). Venter with two white lines enclosing three pairs of black spots in black area (Fig. 321). Anterior lateral eyes 0.5 diameter of anterior median eyes; posterior median and posterior lateral eyes subequal to anterior median eyes. Anterior median eyes their diameter apart, two diameters from laterals. Posterior median eyes slightly more than their diameter apart, three diameters from laterals. The abdomen is elongate, with anterior lateral humps. Total length, 18.0 mm. Carapace, 6.3 mm long, 5.1 mm wide. First femur, 10.5 mm; patella and tibia, 11.3 mm; metatarsus, 11.3 mm; tarsus, 2.3 mm. Second patella and tibia, 10.8 mm; third, 6.0 mm; fourth, 9.9 mm.

Male. Carapace yellow-brown. Legs yellow-brown, not banded. Dorsum of abdomen white; second specimen with a dark folium. Venter with two white longitudinal lines, gray in between. Carapace nearly circular. Anterior lateral eyes 0.5 diameter of anterior median eyes; posterior median eyes subequal to anterior medians; posterior laterals 0.9 diameter. Anterior median eyes 0.7 diameter apart, 0.7 from laterals. Posterior median eyes 1.2 diameters apart, more than two diameters from laterals. The chelicerae are small and reduced. Total length, 6.0 mm. Carapace, 3.2 mm long, 3.2 mm wide. First femur, 4.2 mm; patella and tibia, 4.7 mm; metatarsus, 4.7 mm; tarsus, 1.4 mm. Second patella and tibia, 4.5 mm; third, 2.3 mm; fourth, 3.5 mm.

Note. The palpal embolus of one male is broken off and missing.

Diagnosis. The female can be separated from *Argiope aetherea* by the frame-like black marks and shield-shaped abdomen (Fig. 320). The anterior bulge of



Figures 317–323. *Argiope radon* n. sp. 317–321. Female. 317. Epigynum, ventral. 318. Epigynum, posterior. 319. Epigynum, lateral. 320. Carapace and abdomen. 321. Sternum and abdomen. 322. Left male palpus, mesal. 323. Median apophysis from "below."

Figures 324–328. *Arigope truk* n. sp., female. 324. Epigynum, ventral. 325. Epigynum, posterior. 326. Epigynum, lateral. 327. Carapace and abdomen. 328. Sternum and abdomen.

Figures 329–333. *Argiope ponape* n. sp, female. 329. Epigynum, ventral. 330. Epigynum, posterior. 331. Epigynum, lateral. 332. Carapace and abdomen. 333. Sternum and abdomen.

Scale lines. 0.1 mm, except Figures 320, 321, 327, 328, 332, 333, 1.0 mm.

the epigynum is wider and the rim on each side more curved than that of *A. aetherea*. (Figs. 317–319). The males differ by the median apophysis of *Argiope radon* having a large spur attached to near its bend (Figs. 322, 323).

Natural History. M. H. Robinson and B. Robinson (1980) report threads spanning from riverbank to riverbank above a river nowhere more than 5 m wide. The webs were aggregated and shared structural lines. The stabilimentum was present in only 3 of 32 webs, and one vertical line was broken at the hub; the webs are large (100 × 75 cm), with eccentric hubs in the upper half. Courtship and mating behavior is reported in M. H. Robinson and B. Robinson (1980).

Argiope truk new species

Figures 324–328; Map 5

Holotype. Female from Moen, Truk Island, Caroline Islands, in man-made cave, 12 June 1973, ♀ (J. A. Beatty and J. W. Berry) in the B. P. Bishop Museum, Honolulu. The specific name is a noun in apposition after the type locality.

Description. Carapace light, streaked and covered with white down. Sternum completely yellow-white. Coxae black. Legs light and dark brown, indistinctly banded. Dorsum of abdomen with irregular symmetrical marks forming a frame around light anterior (Fig. 327). Venter contrastingly banded (Fig. 328). Anterior lateral eye diameter equal to radius of others, which are subequal in size. Anterior median eyes 1.8 diameters apart, more than 2.5 from laterals. Abdomen oval without humps or lobes and pointed behind (Fig. 327). Total length, 14.5 mm. Carapace, 5.6 mm long, 4.5 mm wide. First femur, 9.0 mm; patella and tibia, 9.3 mm; metatarsus, 8.9 mm; tarsus, 2.0 mm. Second patella and tibia, 9.0 mm; third, 4.9 mm; fourth, 7.9 mm.

Diagnosis. Argiope truk differs from the sympatric *A. appensa* by the nearly straight rim of the epigynum (Fig. 324), lacking the broken appearance of that in *A. appensa*. The epigynum is like that of *A. aetherea*, but the species differs by not having the posterior tip on the dorsum of the abdomen black, and by having the shape of the abdomen more oval (Fig. 327).

Paratypes. CAROLINE ISLANDS: *Truk Islands.* Moen, on roadside shrubs at night, 11 June 1973, 2♀ (J. W. Berry, J. A. Beatty, MCZ, BC). Mt. Uniböt, Tol Isl., 30 Dec. 1952, ♀, 1 Jan. 1953, ♀ (J. L. Gressitt, BPBM).

Argiope ponape new species

Figures 329–333; Map 5

Holotype. Female from Agricultural Experiment Station, Colonia, Ponape, Caroline Islands, no. BPBM 12513 in the B. P. Bishop Museum, Honolulu. The specific name is a noun in apposition after the type locality.

Description. Carapace dark brown with white down. Sternum yellow-white (Fig. 333). Legs brownish black, not banded. Dorsum of abdomen transversely banded on posterior (Fig. 332; anterior part of dorsum damaged). Venter of abdomen with transverse white bands connecting longitudinal lines. Abdomen is widest anteriorly and lobed posteriorly on the sides (Figs. 332, 333). Total length, 15.8 mm. Carapace, 5.8 mm long, 5.0 mm wide. First leg (missing); second patella and tibia, 10.1 mm; third, 5.6 mm; fourth, 9.2 mm.

Diagnosis. The species differs from others of the *aetherea* group by the dorsal banding on the abdomen, the narrow black and white stripes being of almost equal width (Fig. 332), and by the two white transverse lines connecting the two paraxial ventral lines (Fig. 333). Unfortunately, only one specimen is available, which has the anterior of the abdomen damaged.

Gea C. L. Koch, 1843

Gea C. L. Koch, 1843: 101. Type species by monotypy *Gea spinipes* C. L. Koch from "Puloloz, Os-

tindien" [? Pulo Lozin, southern Burma, now southern tip of Thailand, Gulf of Siam].

Ebaea L. Koch, 1872: 130. Type species *E. praecincta* L. Koch [=*Gea heptagon* (Hentz)] designated by Bonnet, 1956: 1641.

Note. Unfortunately, C. L. Koch's specimen was a juvenile in shrivelled condition, with uncertain locality. Since the generic name *Gea* is in use, it is best to make the neotype for the name of the type species a specimen belonging to a widespread species (see below).

Diagnosis. Gea differs from *Argiope* by having the posterior eyes about equally spaced (Figs. 348, 353); those of *Argiope* have the posterior medians farther from the laterals than the posterior medians from each other. *Gea* differs from both *Argiope* and *Neogea* by having the anterior head region bearing the posterior median eyes swollen (Figs. 334–337). The epigynum is usually weakly sclerotized, the openings sometimes hidden (Figs. 338, 376, 381) and appearing more elaborate and specialized than those of most *Argiope* species. The male palpus has a longer median apophysis (Figs. 375, 388), a more elaborate conductor (Figs. 344, 361, 388), again appearing more specialized than the palpus of *Argiope* species, although I expect that some species are intermediate between the two genera. All *Gea* species are relatively small, females 5 to 9 mm total length.

Coloration. While many *Argiope* species have the carapace covered by silver or white down, this is not usually so in *Gea* (or does it get rubbed off more easily?). The abdomen is less contrastingly marked on the dorsum than in *Argiope* species and often has a black folium at the posterior end (Figs. 348, 353, 358). In place of the two ventral paraxial white lines in *Argiope*, *Gea* species have a series of white splotches (Figs. 342, 354, 372).

Structure. The chelicerae are relatively weak (Figs. 334–337). The abdomen of most species is shield-shaped (rarely oval), widest anteriorly and often with a pair of small anterolateral humps (Figs. 348, 353).

Behavior. We have most knowledge of *Gea heptagon* and *Gea eff. Gea eff* has a stabilimentum (M. H. Robinson and B. Robinson, 1980); *G. heptagon* makes a vertical web low in grass, the orb usually lacking a stabilimentum (Levi, 1968). When disturbed, *Gea heptagon* drops out of the web and rapidly changes color once on the ground (E. Sabath, 1970).

Species and Distribution. There are seven species in the Pacific region (Map 6); one of these species, *G. heptagon*, is also known from the Americas (Levi, 1968), the only *Gea* species occurring in America. Roewer (1942) lists four species from Africa; but these may be misplaced or be synonyms of the widespread *Gea heptagon*.

Misplaced species:

Gea virginis Strand, 1911b: 147. Female holotype from Aru Island in the Senckenberg Museum, Frankfurt, examined, is a *Leucauge*.

KEY TO PACIFIC AREA *GEA* FEMALES

1. Epigynum with a distinct septum visible in ventral view separating two depressions (Figs. 345, 350, 355, 362, 368) 2
– Epigynum without septum visible in ventral view (Figs. 338, 376, 381) 5
2(1). Septum continuing anteriorly into a rim which frames depressions completely as in Figure 350; overhang of depressions transparent (Figs. 350, 351); Burma to New Guinea, Borneo, Philippines (Map 6) ..... *subarmata*
– Septum continuing posteriorly to surround openings as posterior plate (Figs. 345, 355, 362, 365) or not surrounding opening 3
3(2). Septum thick, disappearing anteriorly and transforming posteriorly into hemispherical posterior plate (Figs. 345, 346); New Guinea (Map 6) ..... *argiopides*
– Septum narrow and continuing anteriorly into a transverse rim and posteriorly into the posterior plate (Figs. 355, 362, 365) 4
4(3). Posterior plate wider than long in posterior view (Figs. 363, 366, 369); India, Malay Peninsula, Sumatra, Borneo (Map 6) ..... *spinipes*
– Posterior plate longer than wide with rim visible on each side in posterior view (Fig. 356); New Guinea (Map 6) ..... *eff*

5(1). Epigynum with a transverse anterior lip (Fig. 338); septum visible in posterior view (Fig. 339); widespread (Map 6) ..... *heptagon*

– Epigynum a knob without transverse anterior lip (Figs. 376, 381) 6

6(5). Septum visible in anterior or lateral view only (Figs. 381, 383); eastern Australia (Map 6) ..... *theridioides*

– No septum visible in anterior or lateral view (Figs. 376, 378); New Guinea (Map 6) ..... *bituberculata*

KEY TO PACIFIC AREA *GEA* MALES

(The males of *Gea argiopides*, *G. bituberculata*, and *G. subarmata* are unknown.)

1. Embolus coiling on distal surface of palpus; conductor enclosing and surrounding bulb (Figs. 343, 344); widespread (Map 6) ..... *heptagon*

– Embolus coiling on mesal side of bulb; conductor projecting (Figs. 360, 375, 387) 2

2. Conductor tuberculate (Figs. 387, 388); long median apophysis without spur (Figs. 387, 388); eastern Australia (Map 6) ..... *theridioides*

– Conductor smooth (Figs. 360, 375); median apophysis with spur 3

3. Conductor hiding most of embolus in mesal view (Figs. 360, 375); spur almost as long as median apophysis (Fig. 360); New Guinea (Map 6) ..... *eff*

– Conductor only partly hiding embolus in mesal view (Fig. 375); spur on small thorn on long median apophysis (Fig. 375); India, southeastern Asia, Sumatra, Borneo (Map 6) ..... *spinipes*

Gea heptagon (Hentz)

Figures 334, 335, 338–344; Map 6

Epeira heptagon Hentz, 1850: 20, pl. 3, figs. 5, 6, ♀♂. Type specimen from North Carolina and Alabama, United States, destroyed.

Ebaea praecincta L. Koch, 1872: 130, pl. 10, figs. 2, 3, ♀, ♂. Two female syntypes from Upolu, Samoa in the Zoologisches Museum, Universität Hamburg, examined. NEW SYNONYMY.

Gea praecincta:—Simon, 1895: 765, fig. 844. Roewer, 1942: 746. Bonnet, 1957: 1983. NEW SYNONYMY.

Gea heptagon:—Levi, 1968: 324, figs. 1–24, map 1.

Diagnosis. The female can be separated from other *Gea* species by the shape of the epigynum: a prominent straight rim with a transverse anterior pocket and openings facing posterodorsally (Figs. 338–340).

The male can be separated from other *Gea* species by the apical position of the embolus whose tip is held by a gently curved conductor which surrounds the bulb (Figs. 343, 344).

Variation. Some specimens from Australia have anterior humps on the abdomen, others do not (Fig. 341).

Note. This is the first time that the species has been recorded outside of the Americas. Since it is the only American *Gea*, with several other Australian *Gea* species, I suspect it originally came from Australia. The illustrations were made from a specimen from Darwin, Northwest Territory.

Distribution. Southeastern United States, West Indies (Levi, 1968), South Pacific, Australia (Map 6).

Records. MARIANA ISLANDS: *Saipan.* Sugar King Monument, 30 June 1969, ♀ (E. Sabath, MCZ). CAROLINE ISLANDS: *Truk Isl.* Moen, on abandoned building, 12 June 1973, ♀ (J. A. Beatty, J. W. Berry, BC). AUSTRALIA: *Northern Territory.* Darwin, 3–13 Feb. 1945, ♀, ♂ (B. Malkin, AMNH). *Queensland.* Gordonvale, ♂ (AMS); Rockhampton, 2♀ (ZMH). *New South Wales.* Sydney, ♂ (ZMH).

Gea argiopides Strand

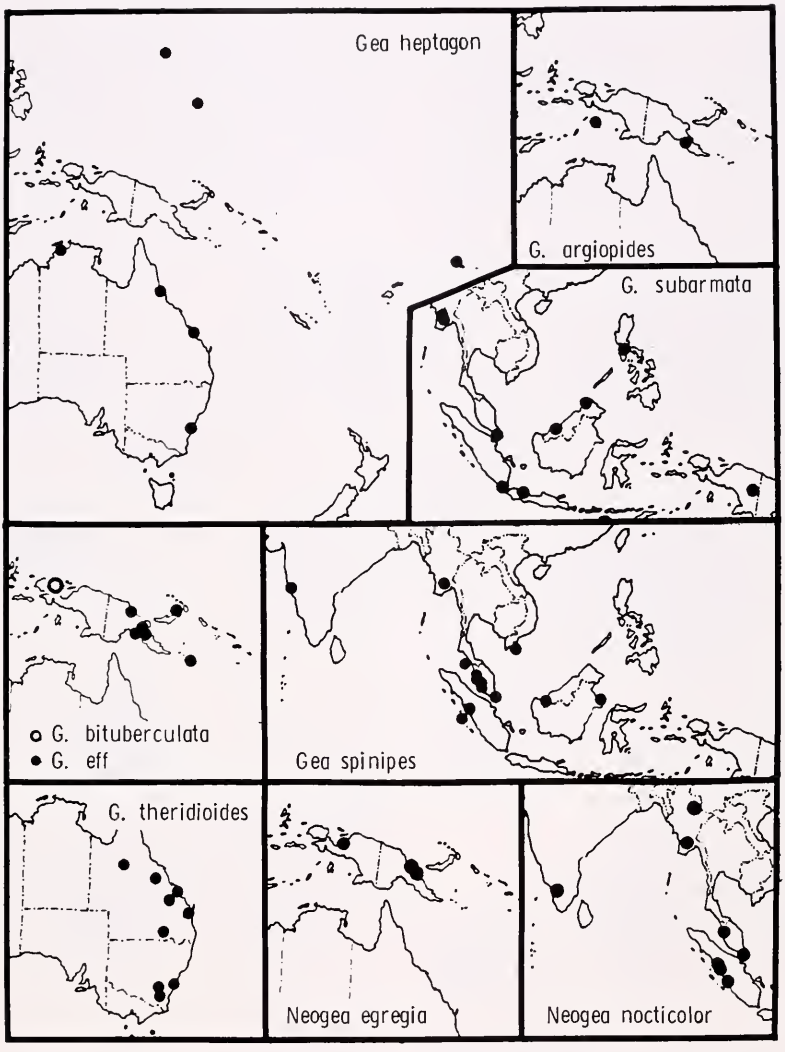
Figures 345–349; Map 6

Gea argiopides Strand, 1911b: 146, pl. 4, fig. 10, pl. 5, fig. 51, ♀. Female holotype from Seltoeti Kobroor, Aru Island in the Senckenberg Museum, Frankfurt, examined. Roewer, 1942: 746. Bonnet, 1957: 1982.

Note. The illustrations were made from specimens from the Central Province, Papua New Guinea.

Diagnosis. Gea argiopides differs from other *Gea* species by the distinct epigynum: a straight anterior edge of the rim, lacking a posterior edge, and a septum continuing posteriorly into a large hemispherical posterior plate (Figs. 345, 346).

Record. PAPUA NEW GUINEA: *Cen-*



Map 6. Distribution of *Gea* and *Neogea* species, and the Pacific distribution of *G. heptagon.*

tral Prov. Sogeri Plateau, near Sogeri, 1000 m, 1 May 1980, ♀ (Y. Lubin, MCZ).

Gea subarmata Thorell

Figures 350–354; Map 6

Gea subarmata Thorell, 1890: 101. Female syntype from Sarawak in the Museo Civico di Storia Naturale, Genova, and two female syntypes from Singapore and two from Java in the Naturhistoriska Riksmuseet, Stockholm, examined. Roewer, 1942: 746. Bonnet, 1957: 1984.

Gea catenulata Thorell, 1898: 339. Female holotype from Teinzo [? Teinsan], Burma in the Museo Civico di Storia Naturale, Genova examined. Roewer, 1942: 745. Bonnet, 1957: 1982. NEW SYNONYMY.

Gea brongersmai Chrysanthus, 1971: 18, figs. 26–29, ♀. Female paratype from Tanah Merah, Star Mountains Exped., West New Guinea in the Rijksmuseum van Natuurlijke Historie, Leiden, examined. NEW SYNONYMY.

Gea corbetti Tikader, 1982: 109, figs. 205–210, ♀. Female holotype from Corbett National Park, Dhikala, Dist. Pauri, Uttar Prades State, India in the Zoological Survey of India, Calcutta, unavailable. NEW SYNONYMY.

Note. The specimens called *G. subarmata* by Kulczyński (1910, 1911) are *Gea eff*; they were misidentified. The type of *Gea brongersmai* Chrysanthus has a slightly wider, shorter septum. Chrysanthus' illustration of the epigynum is poor and does not show the diagnostic transparent overhang of the depression. The illustrations (Figs. 351–354) were made from the holotype of *Gea catenulata*, Figure 350 from a syntype of *G. subarmata*.

Diagnosis. Gea subarmata is distinguished from other species of *Gea* by the rim of the circular epigynum completely surrounding and framing the depression (Figs. 350, 351). The overhanging part of the rim is transparent and thus its edge is quite difficult to see.

Distribution. India, Burma, Philippines, Borneo, to New Guinea (Map 6).

Records. BURMA: Tharrawaddy, 4♀ (Oates, BMNH); 2♀ (Oates, NRS). SINGAPORE: 2♀ (Kinberg, NRS). PHILIPPINES: *Luzon.* Los Baños, ♀ (Baker, MCZ). MALAYSIA: *Sabah.* Manuluk Isl., Kota Kinabalu, 29 July 1979, ♀ (MC). INDONESIA: *Sebesi Isl.*, 1921, ♀ (AMNH). *Java.* 2♀ (Kinberg, NRS).

Gea eff new species

Figures 336–337, 355–361; Map 6

Gea subarmata:—Kulczyński, 1911: 476, pl. 20, figs. 48, 49. Misidentification; not *G. subarmata* Thorell.

Argiope "F":—B. C. Robinson and M. H. Robinson, 1974: 146. M. H. Robinson, Lubin, and B. Robinson, 1974: 126. M. H. Robinson and B. Robinson, 1980: 71, 111, figs. 55–57, ♀.

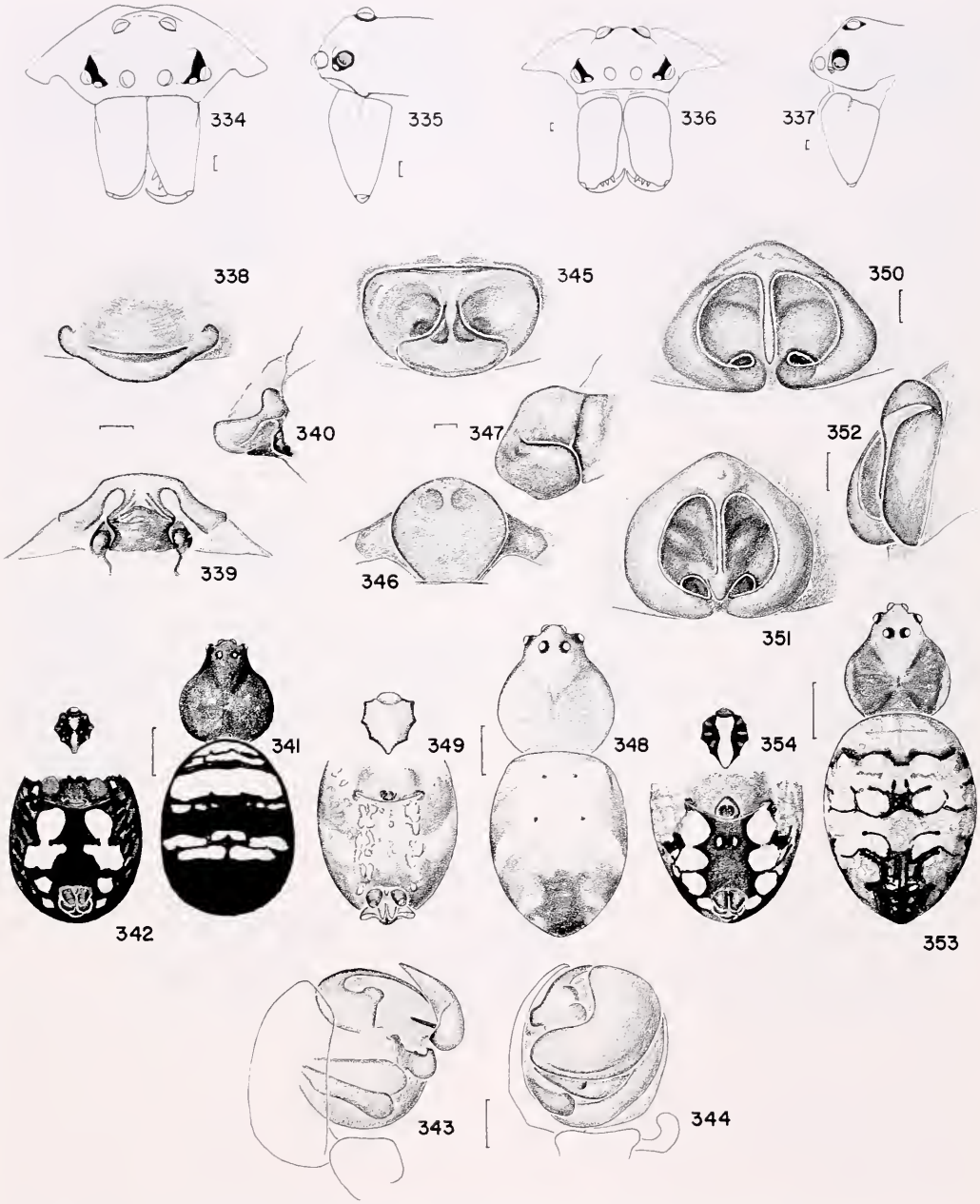
Holotype. Female and three female paratypes and fragments of male from McAdam Park, near Wau, Morobe Province, Papua New Guinea, 12 June 1974 (M. Robinson) in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Female. Carapace brown, head light. Sternum with longitudinal white stripe on black (Fig. 359). Legs banded. Dorsum of abdomen with transverse bands, posterior with black folium (Fig. 358). Anterior lateral eyes 0.5 diameter of anterior medians; others subequal in size. Anterior medians slightly more than their diameter apart, their diameter from laterals. Posterior median eyes slightly more than their diameter apart, the same distance from laterals. Total length, 6.6 mm. Carapace, 3.2 mm long, 2.5 mm wide. First femur, 3.3 mm; patella and tibia, 3.8 mm; metatarsus, 2.9 mm; tarsus, 1.3 mm. Second patella and tibia, 3.8 mm; third, 2.2 mm; fourth, 3.2 mm.

Male. Carapace, sternum, legs beige. Dorsum of abdomen with scattered white pigment spots; indications of a dark folium posteriorly. Venter has white pigment concentrated in two white spots, side by side. Posterior median eyes slightly smaller than anterior medians; anterior laterals 0.5 diameter of anterior medians; posterior laterals same diameter as anterior medians. Anterior medians their diameter apart, 0.5 diameter from laterals. Posterior medians 1.5 diameters apart, 1.5 diameters from laterals. Chelicerae reduced. Total length, 3.0 mm. Carapace, 1.9 mm long, 1.7 mm wide. First femur, 2.2 mm; patella and tibia, 2.5 mm; metatarsus, 2.2 mm; tarsus, 0.9 mm. Second patella and tibia, 2.3 mm; third, 1.3 mm; fourth, 1.8 mm.

Diagnosis. Gea eff can be separated from the other species by the epigynum, whose posterior plate curves into the depression and is deeply hollowed out on each side of the septum (Fig. 355). The palpus differs from that of other species by having a relatively short median apophysis with a long straight side spur from the mesal end (Figs. 360, 361). The conductor tip is large and smooth (Figs. 360, 361).

Natural History. This species has been collected sweeping in coconut plantations and forest. B. C. Robinson and M. H. Robinson (1974) report that *G. eff* builds its web below the upper margins of herb patches in tall grass (M. H. Robinson, Lubin, and B. Robinson, 1974). It has a cruciform stabilimentum whose branches do not cross the hub (M. H. Robinson and B. Robinson, 1980). Courtship and mating are



Figures 334–337. *Gea*, female eye region and chelicerae, face view and lateral. 334, 335. *G. heptagon*. 336, 337. *G. eff.*

Figures 338–344. *Gea heptagon* (Hentz). 338–342. Female. 338. Epigynum, ventral. 339. Epigynum, posterior. 340. Epigynum, lateral. 341. Carapace and abdomen. 342. Sternum and abdomen. 343, 344. Left male palpus. 343. Mesal. 344. Ventral.

Figures 345–349. *Gea argiopides* Strand, female. 345. Epigynum, ventral. 346. Epigynum, posterior. 347. Epigynum, lateral. 348. Carapace and abdomen. 349. Sternum and abdomen.

Figures 350–354. *Gea subarmata* Thorell, female. 350, 351. Epigynum, ventral. 352. Epigynum, lateral. 350. (Sarawak). 351, 352. (Burma). 353. Carapace and abdomen. 354. Sternum and abdomen.

Scale lines. 0.1 mm, except Figures 341, 342, 348, 349, 353, 354, 1.0 mm.

described in M. H. Robinson and B. Robinson, 1980.

Paratypes. PAPUA NEW GUINEA: *Madang Distr.* 10 km N Madang, 20 March 1979, ♀ (H. Levi, Y. Lubin, B. Robinson, MCZ); 40 km S Madang, 21 March 1979, ♀ (H. Levi, Y. Lubin, AMS); near Alexishafen, 23 March 1979, ♂ (H. Levi, B. Robinson, MCZ). *Morobe Distr.* Oomsis, 35 km W Lae-Bulolo road, 26–28 April 1959, ♀ (Archbold Exped., AMNH); Wau, 1200 m, July 1974, ♀ (E. W. Classey, MC). *Central Distr.* Galley Reach. Aroana Estate, 19–25 March 1966, ♀ (G. Bush, MCZ). *Louisiade Archipelago.* Sudest Isl., Sept. 1956, ♀ (Archbold Exped., AMNH). *New Britain.* ♀ (NMW).

Gea spinipes C. L. Koch

Figures 362–375; Map 6

Gea spinipes C. L. Koch, 1843: 101, pl. 823. Shrivelled juvenile from "Puloloz, Ostindien,"* lost, probably destroyed.

Pronous chelifer Hasselt, 1882: 24, pl. 2, fig. 3, pl. 4, figs. 7–10, ♂. Male holotype (without abdomen) from Sumatra in the Rijksmuseum van Natuurlijke Historie, Leiden, examined. NEW SYNONYMY.

Gea decorata Thorell, 1890: 104. Female syntype from Singeibulu, Sumatra in the Museo Civico di Storia Naturale, Genova, examined. Workman, 1896: 23, pl. 23, ♂. Roewer, 1942: 745. Bonnet, 1957: 1982. NEW SYNONYMY.

Gea festiva Thorell, 1895: 166. Two female syntypes from Tharawaddy, Burma in the British Museum, Natural History, and one female from same locality in Naturhistoriska Riksmuseet, Stockholm, examined, one female syntype from Singapore in the National Museum of Ireland, not examined. Roewer, 1942: 745. Bonnet, 1957: 1982. NEW SYNONYMY.

Gea festiva nigrifrons Simon, 1901: 59. Female type from Yala, near Battani, Thailand and Bukit Bekit, Jalor, lost; not in Paris or London collections.

Neotype. Female from Fraser's Hill, Malaysia, 1 June 1981 (W. C. Sedgwick) in the Museum of Comparative Zoology.

Notes. The generic name *Gea* has been used since the 1890's, although Koch's description of *G. spinipes*, the type species of the generic name, is not recognizable. For stability's sake, a neotype is here designated from Malaysia belonging to the commonest and most widespread southeast Asian species of *Gea*. Simon and Thorell cite the name *Gea spinipes*, but had apparently no determined specimens of this species.

Pronous chelifer had previously been synonymized with *Argiope catenulata* (Roewer, 1942).

The illustrations (Figs. 362–364, 371, 372) were made from specimens from Karnatake, India; Figures 365–367, 373, 374 from a syntype of *Gea festiva* Thorell from Burma; Figures 368–370 from a syntype of *Gea decorata* Thorell, Figure 375 from a specimen from Vietnam.

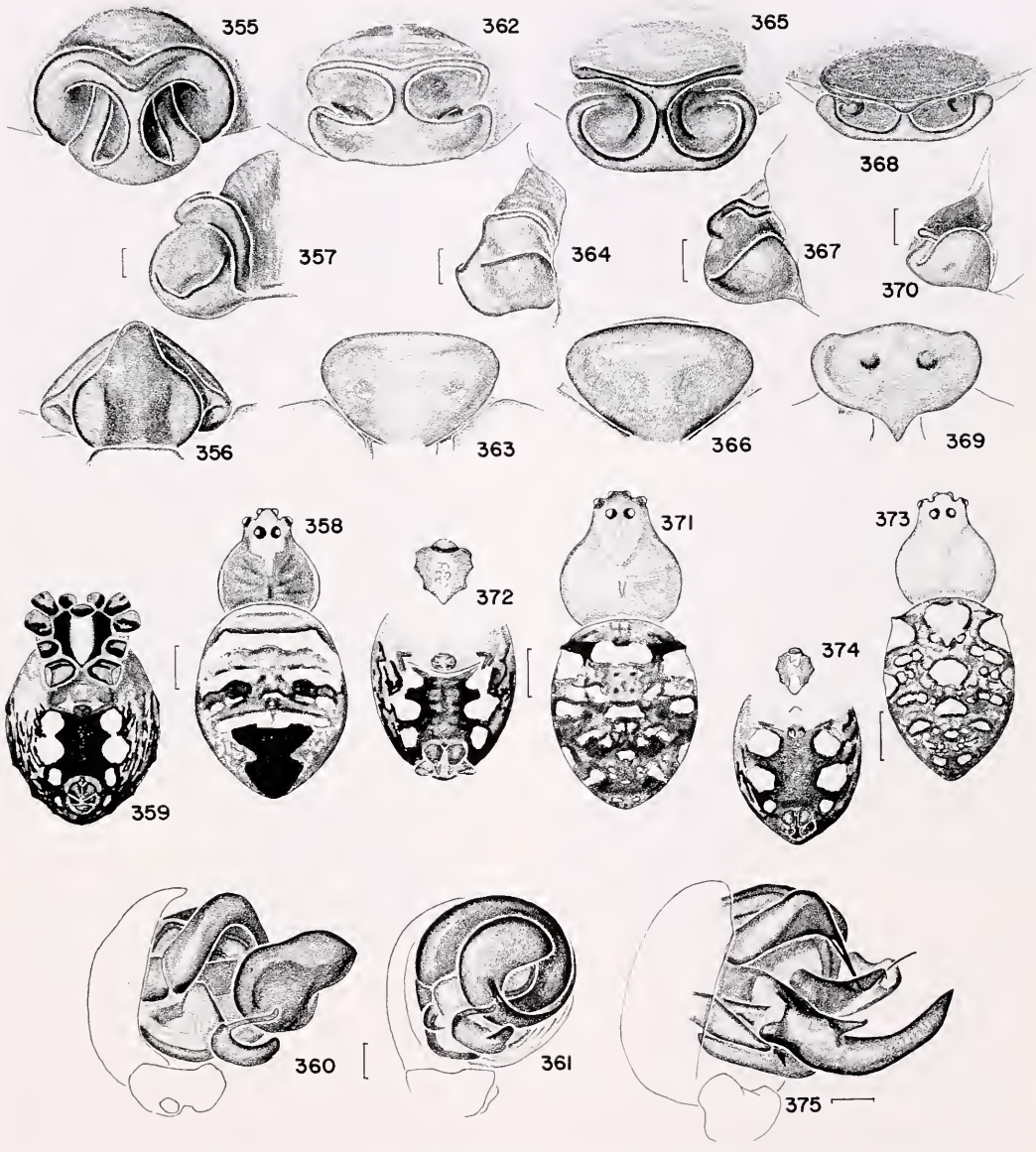
Diagnosis. Gea decorata can be separated from other *Gea* species by the dorsal abdominal pattern having a median row of black-framed white patches, and smaller white patches to the sides (Figs. 371, 373). It differs from *G. eff* by having the posterior plate of the epigynum wider than long (Figs. 363, 366, 369); its sides often completely fill the depression and curl within it (Fig. 365). The epigynum of *Gea decorata* could be confused with that of *Argiope doboensis* and *A. dietrichae*, but the larger posterior median eyes and abdomen pattern separate the species.

The male palpus, unlike that of other *Gea* species but like *G. theridioides*, has an enormous median apophysis projecting under the conductor (Fig. 375). It differs from that of *G. theridioides* by having a smaller conductor (Fig. 375).

Distribution. Indochina to India, Indonesia, Borneo (Map 6).

Records. VIETNAM: Con Son Isl., Nov. 1966, ♂ (MCZ). BURMA: Tharrawaddy, ♀ (Oates, NRS). MALAYSIA: *Malay Peninsula. Perak*, Maxwell's Hill, 17 Feb. 1974, ♀ (W. C. Sedgwick, MCZ); Fraser's Hill, 8 June 1976, ♀ (W. C. Sedgwick, SC); Johor [Johore], Layang-Layang, remnant jungle, 25 July 1979, ♀ (J. and F. Murphy,

* Ostindien—Name für Vorder-u. Hinterindien und den Malaiischen Archipel [Name for India, Indochina, and Indonesia] (Knaurs Lexikon, 1978 edit.). The locality is most likely in Malaysia or Indonesia because "Pulo" = island; it may have been Pulo Lozin (southern Burma, now southern Thailand), the "in" (German "In." = Island) having been dropped.



Figures 355–361. *Gea eff* n. sp. 355–359. Female. 355. Epigynum, ventral. 356. Epigynum, posterior. 357. Epigynum, lateral. 358. Carapace and abdomen. 359. Sternum and abdomen. 360, 361. Left male palpus. 360. Mesal. 361. Ventral.

Figures 362–375. *Gea spinipes* C. L. Koch. 362–374. Female. 362, 365, 368. Epigynum, ventral. 363, 366, 369. Epigynum, posterior. 364, 367, 370. Epigynum, lateral. 362–364. (India). 365–367. (Burma). 368–370. (Sumatra). 371, 373. Carapace and abdomen. 372, 374. Sternum and abdomen. 371, 372. (India). 373, 374. (Burma). 375. Left male palpus, mesal.

Scale lines. 0.1 mm, except Figures 358, 359, 371–374, 1.0 mm.

MC). *Selangor*. Kepong, 22 April 1921, ♀ (H. C. Abraham, ZRC); Port Dickson, Dec. 1924, ♀ (ZRC). *Sarawak*. Kuching, 4 April 1978, ♀ (K. Krishna, AMNH). SINGAPORE: ♀ (Workman, NRS); mangroves, 21 May 1922, ♀ (H. C. Abraham, ZRC). INDIA: Karnstaka, Dandeli [railroad station, 15°15′N, 74°37′E], 530 m, Nov. 1979, ♀ (W. Eberhard, MCZ). INDONESIA: *Sumatra*. Siberut Isl., Sept. 1924, ♀ (C. B. Kloss, N. Smedley, ZRC). *East Borneo* [Kalimantan]. Maratoea Isl. [Maratua], ♂ (E. Mjöberg, NRS).

Gea bituberculata (Thorell)

Figures 376–380; Map 6

Ebaea bituberculata Thorell, 1881: 60. Female holotype from Hatam, Arfak Mountains, southwest of Dorei, New Guinea [Dore Baai, Vogelkop Peninsula, West Irian] in the Museo Civico di Storia Naturale, Genova, examined.

Gea bituberculata:—Roewer, 1942: 746. Bonnet, 1957: 1982.

Note. The illustrations were made from the holotype.

Diagnosis. This small species differs from *Gea theridioides* by the shape of the epigynum: the septum has expanded and wrapped around other features, including the anterior face of the epigynum (Figs. 376–378).

Gea theridioides (L. Koch)

Figures 381–388; Map 6

Ebaea theridioides L. Koch, 1872: 132, pl. 10, fig. 4, ♀. Female holotype from Port Mackay, Queensland, Australia in Zoologisches Museum, Universität Hamburg, lost. One female from Peake Downs [Queensland, Australia] in the Godeffroy collection here designated lectotype in the Naturhistorisches Museum, Wien, examined.

Argiope curvipes Keyserling, 1886: 135, pl. 11, fig. 1, ♂. Male holotype from Gayndah, Peake Downs [southeastern Queensland] in the British Museum, Natural History, examined. NEW SYNONYMY.

Gea theridioides:—Roewer, 1942: 746. Bonnet, 1957: 1984. Mascord, 1970: 78, pl. 35, fig. 137, ♀.

Notes. The specimen marked lectotype had been registered as a type in the catalog of the Naturhistorisches Museum, Vienna. Males and females have not been collected together, thus there is some doubt as to whether they belong together.

The female genitalia illustrations (Figs. 381–383) were made from a specimen from Sydney; Figure 384 from a specimen from Currawong. Three other females with the Currawong specimen had the posterior plate as in Figure 382. The abdomen may be oval or with anterior humps (Fig. 385). The male genitalia illustrations (Figs. 387, 388) were made from a specimen labeled *E. praecincta* from Sydney in the British Museum, Natural History collection.

Diagnosis. The female can be separated from other *Gea* by the unusually shaped epigynum: the posterior plate continues ventrally into a flat plate enclosing a median wrinkled septum (Figs. 381–384), visible from anterior or the sides. The male, unlike other species, has sculpturing on the outside of the tip of the conductor and the median apophysis is a long, worm-shaped structure without a spur (Figs. 387, 388).

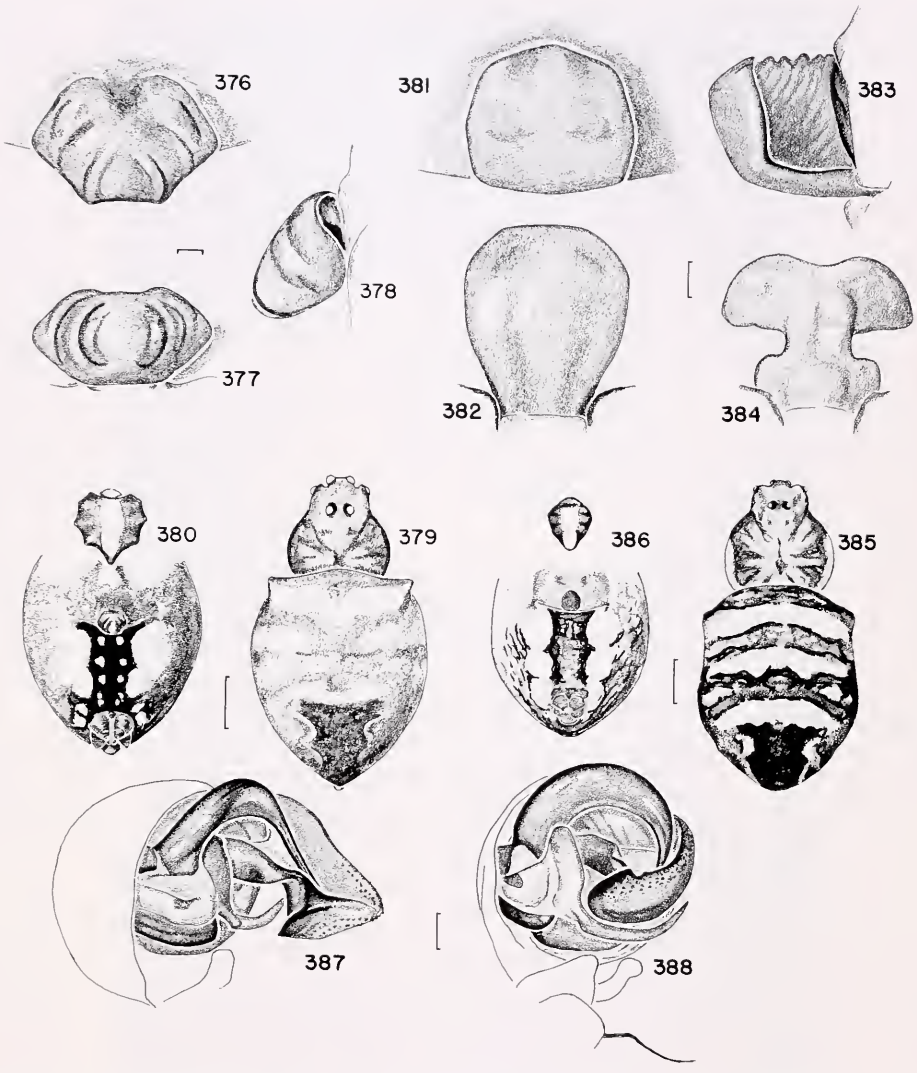
Distribution. Queensland, New South Wales (Map 6). Roewer (1942) reports this species from New Guinea and Samoa, probably an error.

Records. AUSTRALIA: *Queensland*. Rockhampton, ♀ (ZMH); Peake Downs, ♀ (ZMH); ♀ (NMW); Gayndah, ♀ (ZMH); ♀ (NMW); Colosseum, Nov., ♀ (E. Mjöberg, NRS). *New South Wales*. Wyangarie, ♀ (AMS); Boggabilla, 10 March 1970, ♀ (M. J. Cann, AMS); Currawong, 2 Oct. 1965, ♀♀ (R. Mascord, AMS); Sydney, ♂ (BMNH); ♀♀, juv. ♂ (ZMH). *Australian Capit. Terr.* Canberra, 6 April 1963, ♀ (C. R. MacLellan, CSIRO), 7 March 1970, ♀♀ (H. Evans, AMS).

Neogea new genus

Type species. *Araneus egregius* Kulczynski. The gender is feminine.

Diagnosis. *Neogea* differs from *Argiope* by having the posterior eyes about equally spaced, the medians the same dis-



Figures 376–380. *Gea bituberculata* (Thorell), female. 376. Epigynum, ventral. 377. Epigynum, posterior. 378. Epigynum, lateral. 379. Carapace and abdomen. 380. Sternum and abdomen.

Figures 381–388. *Gea theridioides* (L. Koch). 381–386. Female. 381. Epigynum, ventral. 382, 384. Epigynum, posterior. 383. Epigynum, lateral. 381–383. (Sydney, Australia). 384. (Currawong, Australia). 385. Carapace and abdomen. 386. Sternum and abdomen. 387, 388. Male left palpus. 387. Mesal. 388. Ventral.

Scale lines. 0.1 mm, except Figures 379, 380, 385, 386, 1.0 mm.

tance from each other as from the posterior laterals. *Neogea* differs from both *Gea* and *Argiope* by having the head region of the carapace behind the eyes swollen (Figs. 390, 392), the epigynum weakly sclerotized (Figs. 393, 394, 398, 399, 400, 401), and the palpal embolus one piece sitting on the tegulum (Figs. 397, 406) rather than being attached to an intermediate sclerite, the stipes.

Coloration. All species have the carapace black with white setae covering the head and sometimes the sides of the thorax. The abdomen is black with paired and median white or silver patches (Figs. 395, 402, 404). The venter has paraxial white marks (Figs. 396, 403, 405) as in *Argiope*, not like the splotches of *Gea*.

Structure. The chelicerae are quite strong, with a distinct proximal condyle (Figs. 389–392). The abdomen of both species is drawn out posteriorly and overhangs the spinnerets (Figs. 396, 403, 405). The palpus of *N. egregia* has a twisted flap at the base of the embolus (Fig. 397). Perhaps this breaks off when mating and plugs the epigynum. If this is the case, the palpus of *N. nocticolor* examined might be of a mated male and that of *N. egregia* of a virgin male.

Behavior. Neogea females are known to decorate their webs with egg-sacs (Sherriffs, 1928) (Plate 2). Also, as in *Gasteracantha*, the frame lines have tufts of silk (M. H. Robinson, personal communication).

Species. There are only two species: *N. nocticolor* and *N. egregia*.

Distribution. India to New Guinea.

KEY TO SPECIES OF *NEOGEA*

1. Males 2
– Females 3
2(1). Conductor curved and with pointed tip (Fig. 406); India, Burma to Sumatra (Map 6) ..... *nocticolor*
– Conductor straight with a distal notch (Fig. 397); New Guinea (Map 6) ..... *egregia*
3(1). Posterior median eyes appearing large, separated by a distance equal to 1.5 times their diameter (Figs. 391, 392, 402, 404); India, Burma to Indonesia (Map 6) ..... *nocticolor*
– Posterior median eyes small, separated by a distance equal to two diameters (Figs. 389, 390, 395); New Guinea (Map 6) ..... *egregia*

Neogea egregia (Kulczynski) new combination

Figures 389, 390, 393–397; Map 6

Araneus egregius Kulczynski, 1911: 479, pl. 20, fig. 51, ♀. Female holotype from Napan, West Irian in the Polish Academy of Sciences, Warsaw, examined. Roewer, 1942: 827. Bonnet, 1955: 499.

Diagnosis. This species is black except for the head and the white patches on the abdomen (Figs. 395, 396). The female differs from *N. nocticolor* by being larger in size and by having relatively smaller eyes (Fig. 395).

The male has a heavier embolus (Fig. 397) than the male of *N. nocticolor*, a twisted sclerite near the base of the embolus, and the spur of the median apophysis curved up toward the tip of the embolus (Fig. 397).

Records. PAPUA NEW GUINEA: *Morobe Distr.* Oomsis, near Lae, 7 Dec 1979, ♀ (M. Robinson, MCZ); Buso, 4 May 1979, ♂ (M. Robinson, MCZ).

Neogea nocticolor (Thorell) new combination

Figures 391, 392, 398–406; Map 6

Gea nocticolor Thorell, 1887: 170. Two female syntypes from Bhamo, Burma in the Zoologisches Museum, Universität Hamburg, examined.

Gea guttata Thorell, 1890: 107. Juvenile holotype from Sungeibulu [Sungaibulu], Sumatra in the Museo Civico di Storia Naturale, Genova, examined. NEW SYNONYMY.

Gea lugens O. P.—Cambridge, 1899: 520, pl. 29, fig. 3, ♀. Female holotype from Singapore in the Hope Entomological Collections, Oxford University, examined. NEW SYNONYMY.

Gea diadema Hogg, 1920: 92, pl. 9, fig. 6. Female holotype in poor condition from Sungei Kumbang [Kambang], Korinchi Peak [Kerintji], 1400 m, West

Plate 2. *Neogea egregia* (Kulczyński). Above, female and male. Below, female from New Guinea in web having a stabilimentum and four egg-sacs on a line above (photo M. Robinson).

Sumatra in the British Museum, Natural History, examined. NEW SYNONYMY.

Argiope lalita Sherriffs, 1928: 186, figs. 3–7, ♀♂. Male holotype without palpi, two female paratypes from Charlotte Estate, Sidapur, S. Coorg [West of Mysore, Mysore State], India in the British Museum, Natural History, examined. Roewer, 1942: 738. Bonnet, 1955: 687. NEW SYNONYMY.

Notes. The type of *Gea guttata* is a juvenile, 4.3 mm total length, with the same diagnostic coloration, white head setae and posterior median eyes as in *G. nocticolor* Thorell.

The illustrations (Figs. 398, 399, 402, 403) were made from the paratype of *A. lalita*; Figures 400, 401, 404, 405 from the holotype of *Gea lugens*.

The male was not collected with a female; it is all black, except for the proximal ends of the femora (which are also light in females). None of the legs of the male are modified.

The male holotype of *A. lalita* has the distal article of both palpi missing, and Sherriffs' illustration shows only the palpal tibia. The abdomen shape of the syntypes of *G. nocticolor* is more like that of *A. lalita*: drawn out behind and with two small anterior humps on the dorsum, and three posterior white wedge-shaped patches on the abdomen.

Diagnosis. Neogea nocticolor differs from *N. egregia* in having larger, more closely spaced eyes (Figs. 402, 404). The male differs from that of *N. egregia* by the longer, more slender embolus and conductor, and by the shape of the median apophysis, which has a filiform spur extending in a proximal direction (Fig. 406).

Distribution. India, Burma to Sumatra (Map 6).

Records. BURMA: Tharrawaddy, ♀ (Oates, BMNH); Bhamo, 3♀ (NRS). MALAYSIA: *Malay Peninsula*. Genting, 18–22 Aug. 1979, ♂ (F. Murphy and J. Murphy, MC). INDONESIA: *Sumatra*. Fort de Kock [Bukittinggi], ♀♀ (Jacobson, NMW).

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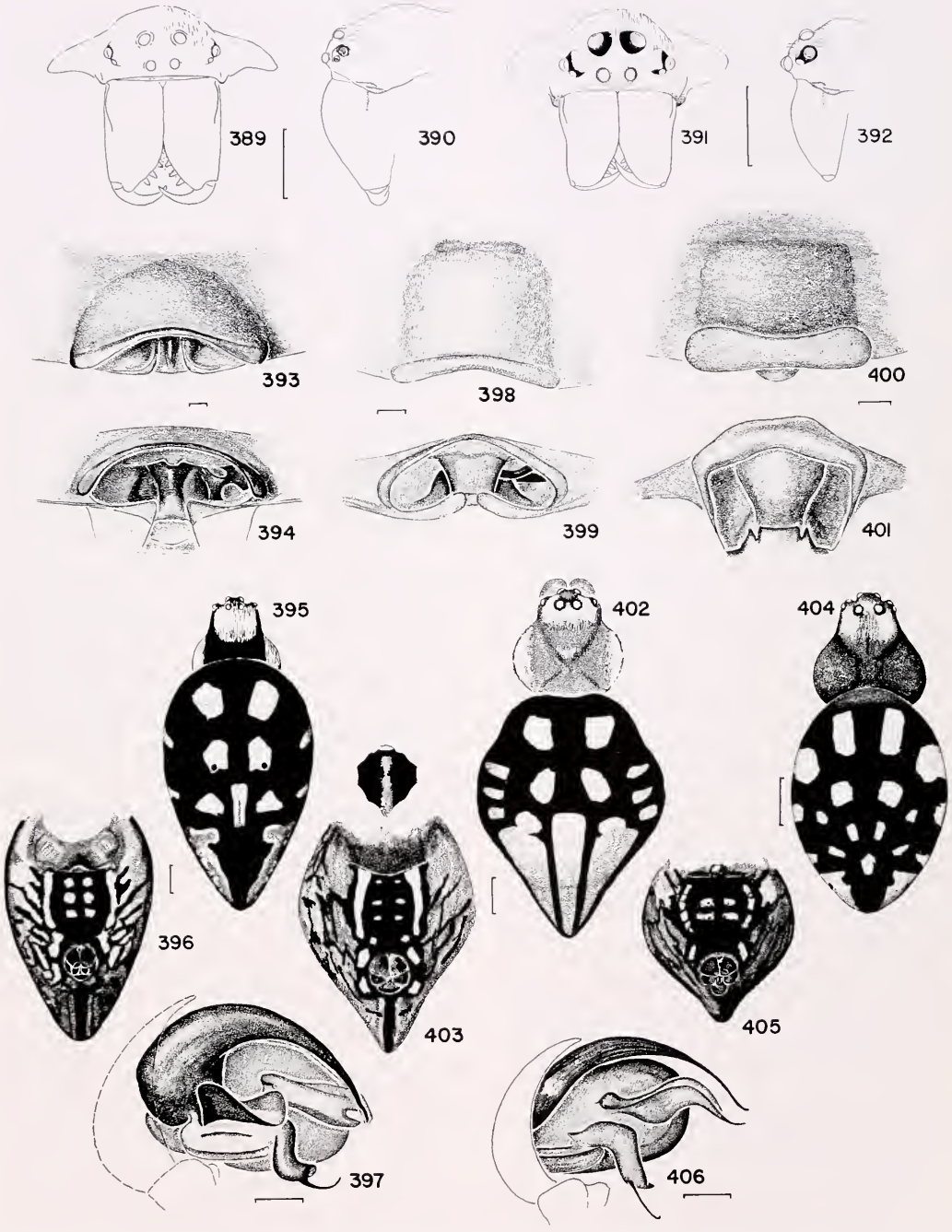

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Relationships of the Neon Tetras, A Group of South American Freshwater Fishes (Teleostei, Characidae), with Comments on the Phylogeny of New World Characiforms

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RELATIONSHIPS OF THE NEON TETRAS, A GROUP OF SOUTH AMERICAN FRESHWATER FISHES (TELEOSTEI, CHARACIDAE), WITH COMMENTS ON THE PHYLOGENY OF NEW WORLD CHARACIFORMS

STANLEY H. WEITZMAN[1] and WILLIAM L. FINK[2]

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ABSTRACT. The history of the classification and the relationships of the American Characidae is reviewed in terms of phylogenetic principles. Current characid systematics is found unstable and unsatisfactory from typological and phylogenetic points of view. We predict that the classification of the American characids and that of all characiforms will be subject to much reinterpretation and rearrangement through future phylogenetic analyses.

The three known species of neon tetras are used as an example of phylogenetic analysis within the American Characidae. This analysis exemplifies the difficulties of an initial phylogenetic study of a taxon with many ill-defined subgroups.

These three species previously were placed in two characid subfamilies and three genera as follows: *Hyphessobrycon simulans*, the green neon, in the Tetragonopterinae; *Cheirodon axelrodi*, the cardinal tetra, and *Paracheirodon innesi*, the neon tetra, in the Cheirodontinae. Several synapomorphies were found to unite all three species, which are herein placed in *Paracheirodon*. The interrelationships among the three neon tetras are not resolved.

INTRODUCTION

The Characidae comprises the largest part of a group of freshwater fishes, the Characiformes, whose living representatives are endemic to Africa and South and Central America. American characids are found from southern Argentina and Chile in South America north to the Mexico-United States border area in North America. The greatest concentration of species occurs in the Amazon basin, the largest geographic area. There are fewer species to the north in the Orinoco basin and to the south in the Paraná-Paraguay river system. Still fewer species occur in the numerous smaller drainage basins in Central America and peripheral to these three large river systems in South America. By the latest account, Géry (1977: 13–16), the American part of the family consists of 12 "subfamilies" and about 700 species, excluding Serrasalminae and Characidiinae, both sometimes included within the Characidae. The phylogeny of these

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"subfamilies" and their relationships to other characiforms are poorly understood.

Systematists studying American characids owe much to the pioneering studies of Eigenmann and his students early in this century. The system of characid classification inaugurated by Eigenmann has formed the framework within which nearly all subsequent research has been done. But there are serious shortcomings with that system, acknowledged by Eigenmann (1917: 43–49), and in recent years there has been some movement toward a different approach to the problems recognized by Eigenmann. Current characid classification is neither phylogenetically nor typologically useful. In the following pages we reexamine the basis for traditional classification of the group, rooted in Eigenmann's concepts of systematic ichthyology, and discuss the approaches several more recent authors have brought to bear on the problem. We propose and discuss the implications of a phylogenetic approach to characid relationships, and present a phylogenetic analysis of a small but representative characid group, the neon tetras.

Many groups of characiforms, including the American characids, include species whose members are of very small size, 12 to 25 or 30 mm in standard length (SL). Many of these species exhibit paedomorphic features, such as reduction in the extent and surrounding ossification of the laterosensory system and reduction in tooth cusp number. The problems of attempting to recognize and diagnose genealogical lineages in a group where small size and reductive features are so common is also treated.

METHODS

The analysis used here is phylogenetic, basically that of Hennig (1966). Much discussion and some modification of Hennig's views have occurred since 1966. The reader is referred to Farris (1978, 1979), Cracraft and Eldredge (1979), Eldredge and Cracraft (1980), Hull (1980), and Wiley (1981), for reviews of recent theoretical and practical views regarding phylogenetic systematics and cladistics.

Counts and measurements follow Fink and Weitzman (1974) unless otherwise explained in the text. All measurements are given as a percent of standard length except those subunits of the head which are a percent of head length.

The synonymies are limited to the original descriptions, accounts of the discovery of the neon tetras, morphological and systematic reports, and aquarium literature accounts providing new name combinations. Most aquarium literature is not cited.

The following abbreviations are used for institutions:

ANSP—Academy of Natural Sciences of Philadelphia
BMNH—British Museum (Natural History), London
CAS—California Academy of Sciences, San Francisco [catalog numbers may read CAS(IUM), formerly of Indiana University, or CAS(SU), formerly of Stanford University]
EPA—Fundação de Amparo à Pesquisa do Estado de São Paulo, Expedição Permanente da Amazônia, São Paulo
FMNH—Field Museum of Natural History, Chicago
INPA—Instituto Nacional de Pesquisas da Amazonia, Manaus
MBUCV—Museo de Biologia, Instituto de Zoologia Tropical, Universidad Central de Venezuela, Caracas
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge
MZUSP—Museu de Zoologia da Universidade de São Paulo, São Paulo
NRM—Naturhistoriska Riksmuseet, Stockholm
USNM—United States National Museum, the collections in the Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Other abbreviations used are:

SL—Standard length
spms—specimens

The species and specimens other than neon tetras examined for this investigation are listed in Appendix 1. The neon tetras are listed in the species accounts.

In the lists of specimens examined, locality information follows the following format: the country is given first in its English form followed by the state, department, or district in the language of the country. This is followed by the specific locality.

SYSTEMATICS OF THE AMERICAN CHARACIDAE

The history of American characid systematics was summarized by Eigenmann (1917) and updated by Weitzman (1962). Since the latter paper appeared, classification within the family has been discussed by several authors, including Roberts (1973), Fink and Weitzman (1974), Rosen (1970, 1972), and Géry (1977). None of the authors subsequent to Eigenmann (1917) has been able to treat adequately the various problems brought forth in that seminal paper. As we will make clear below, we think that progress has been hindered by the kinds of systematic approaches that were employed. It would be useful at this point to summarize Eigenmann's comments, since he was particularly perceptive about aspects of evolution that interest systematic theorists today.

Eigenmann, in a series of papers published early in this century, greatly expanded our knowledge of the complexity of the characid fauna. He was the first author to consider to any appreciable extent the evolutionary relationships of the numerous genera of the American characids. In earlier papers, Eigenmann and his students followed the ichthyological standards of the day and proposed genera based on obvious differences among morphological features. Eigenmann (1914: 23) noted that many characid genera appear polyphyletic. The problem of generic and subfamily relationships came to be one of his primary concerns when he attempted a broad synthesis of his knowledge of American characiforms in 1917. Eigenmann clearly understood the differences between what are now called phylogenetic and grade concepts of classification. Eigenmann (1914: 23) stated: "We recognize two types of genera, one a group of closely related species, descended from a common ancestor and having certain distinguishing characters in common. . . . The other, a polyphyletic type, consists of species having a certain combination of definite characters in common which easily distinguish members of the genus, but which, instead of indicating a single ancestral line from which the species have diverged, are acquired possibly one at a time along distinct lines converging to a common definition. Sometimes the polyphyletic origin can be detected, sometimes not." Eigenmann (1917: 48) came to describe the genera of the Tetragonopterinae as "an interlacing fabric rather than a branching tree." Many of the characters utilized by Eigenmann and his students are those used traditionally as "generic characters" by ichthyologists working with other groups of fishes then and today. Despite Eigenmann's warnings of serious problems for the recognition of characiform genera based on these characters, most subsequent ichthyologists have continued to use this system of names, concepts, and categories for characids at the generic and subfamilial levels. We would here point out that we believe there is nothing inadequate or "wrong" with the characters used; rather, it is how they have been used and interpreted that has been and still remains the problem. Myers (*in* Eigenmann and Myers, 1929: 546) pointed out that "We do not yet have a key to the mensuration of phylogenetic differentiation in the tetragonopterid characins, and until we do it would seem the best course to follow the existing method [re-

ferring to the Eigenmann system of genera, subfamilies, and usage of characters]." Often more recent ichthyologists have tried to "fit" new species and genera into Eigenmann's system by a rigid use of Eigenmann's "generic characters" as set forth in "The American Characidae" (Eigenmann, 1917: 42). Since many of these newly discovered species did not "fit" well into the system, a proliferation of new generic names ensued. Examples include Schultz (1956) and Géry (1960a,b; 1963; 1965a,b; 1966a,b; 1977). In our opinion this procedure is now leading to problems in the usefulness of characid genera as either monophyletic or typological entities. A rigid use of certain characters as always significant at the generic level is producing chaos in the classification of characids.

Eigenmann (1915: 3 and 10–11) and Böhlke (1952: 794) pointed out the possible or probable polyphyly of the cheirodontine characids. This suggestion was further supported by Weitzman (1962: 5), Géry (1977: 543), Vari and Géry (1980: 80), and especially by Fink and Weitzman (1974: 1). Ellis (*in* Eigenmann, 1918: 135), in referring to the tetragonopterine genera *Hemigrammus* and *Hyphessobrycon*, stated the following: "It seems quite certain that these genera are of polyphyletic origin, that several sections have been and are arising independently from *Astyanax* and *Moenkhausia* and probably other genera. These genera (*Hemigrammus* and *Hyphessobrycon*) are conveniences rather than entities." We think these genera are no longer "conveniences." Their typological convenience is at an end because it often conflicts with information from additional characters and consequent ideas about relationships. For example, Böhlke (1955: 233–234), in a discussion of the relationships among some species of *Hemigrammus* and *Hyphessobrycon*, found an analysis of their relationships difficult and ambiguous. In that contribution Böhlke described a new species, *Hemigrammus mimus*, which, on the basis of characters employed by Ellis (*in* Eigenmann, 1918: 133–135) to define *Hemigrammus* and *Hyphessobrycon*, would have to be placed in *Hyphessobrycon*. In view of other characters, Böhlke placed the fish in *Hemigrammus*, predicting that it is most closely related to a known species of *Hemigrammus*. Thus, Böhlke refused to follow the traditional use of a character (presence of caudal-fin squamation) that always had been considered as having "generic value."

The first explicitly phylogenetic study of a characid group is that of Rosen (1972) on *Bramocharax*. He studied the relationships of the species and subspecies in the genus and compared them with species in the tetragonopterine genera *Astyanax*, *Moenkhausia*, *Hemigrammus*, *Deuterodon*, *Bryconamericus*, and *Hemibrycon*. Comparisons apparently were limited to these genera because of the similarity to them of the most primitive *Bramocharax* species. Rosen's conclusion, based on shared unique characters, was that *Bramocharax* is monophyletic and represents the sister group to some lineage within *Astyanax*. The similarity of primitive *Bramocharax* species to *Astyanax* species is so great that Rosen questioned the recognition of *Bramocharax* as distinct from *Astyanax*. Rosen left unanalyzed the implication of his study that *Astyanax* is paraphyletic when *Bramocharax* is recognized.

Roberts (1973) attempted an analysis of the relationships among three genera of presumed glandulocaudine characids of the Guayas basin in western Ecuador. He evaluated certain features on the basis of whether they were primitive, reductive, labile, or specialized. Although he did not define or use characters according to phylogenetic methodology, Roberts (1973: 512) emphasized that of his four categories, specialized characters "are most important in determining relationships." Specialized characters were defined as

originating only once and "... incapable of having originated independently." Roberts noted that the generic classification in Eigenmann's "The American Characidae" is based largely on reductive and labile characters, which Roberts did not consider specialized according to his concepts. In his study Roberts came to the conclusion that none of the osteological characters that he examined could be used as evidence to support his original hypothesis that the "... Guayas glandulocaudins are an autochthonous monophyletic lineage and had *Bryconamericus*-like ancestors." He further concluded that these characters and many others found in characids are unlikely to be useful in studies of phylogenetic relationships because of their lability or their reductive nature. We suspect he came to this judgment because he assumed the species represented an autochthonous radiation without investigating the possible relationships of the three genera with other glandulocaudines outside the Guayas basin, and also because he did not investigate the characters he used in sufficient detail. Our primary criticism of Roberts' analysis is that he seems not to have considered the fact that "labile or reductive" characters may be indicative of monophyly at some taxonomic level even though they may not be significant at the levels under study.

Fink and Weitzman (1974: 4–5) discussed the traditional use of so-called "generic" characters, including lateral-line length, tooth-cusp morphology, procurrent caudal-fin rays, and caudal-fin squamation. Lateral-line length had traditionally been used to "recognize" *Odontostilbe* as different from *Cheirodon*. Fink and Weitzman found, however, that lateral-line length was variable in *Cheirodon dialepturus* Fink and Weitzman and *C. affinis* (Evermann and Goldsborough) to such an extent that in some populations of each species some individuals were "*Odontostilbe*" while others were "*Cheirodon*." Since lateral-line length was the only character which distinguished *Odontostilbe* from *Cheirodon*, the former name was synonymized with the latter. A similar approach was used with the other characters listed above, resulting in synonymizing of *Pseudocheirodon* and *Compsura* with *Cheirodon*. These actions were taken by Fink and Weitzman (1974) to eliminate clearly typological genera whose diagnostic features were no longer useful to pigeonhole characid species.

Subsequently Géry (1977: 554–555) suggested that this practice, if carried to its logical extreme, would result in "lumping" of all "tetragonoterine" genera into a single genus represented by the oldest available name, *Tetragonopterus*. Ulrey (1895) once did what Géry suggested. The species treated by Ulrey previously had been placed in six genera, with most of them in *Tetragonopterus*. Ulrey (1895: 262) cites the variability of the lateral line in given species as one of his reasons for an inclusive genus *Tetragonopterus* and therefore the doubtful significance of this "generic" character. By today's standards, this approach is an oversimplification of a complex problem. Reduction in pored lateral-line length could be variable in one species of a given monophyletic line but constant within another monophyletic line and therefore useful as a synapomorphy delineating that particular lineage. It may be that *Odontostilbe*, the type of which is the Peruvian *Cheirodon fugitiva* (Cope), might still be a recognizable, monophyletic genus. However, since the sole character upon which it was based has been shown to be invalid at the level at which it has been applied, recognition of *Odontostilbe* would require: (1) a detailed study of the species of *Cheirodon* possibly related to *C. fugitiva* to determine if there are characters which could define a monophyletic group; (2) a study of the phylogenetic relationships of all of the species currently placed in *Cheirodon* to determine if *Cheirodon* would be paraphyletic as a consequence of removing some species

of *Cheirodon* to the genus *Odontostilbe*. Géry, *in* Vari and Géry (1980: 81), now seems to accept the reasons for not recognizing *Pseudocheirodon* and *Compsura*.

The most serious problem we now find with the work of Fink and Weitzman (1974) is its lack of rigorous analysis of relationships. Statements referring to "relationships" made by them are unsubstantiated by presentation of putative synapomorphies. For example, on page 25 they considered *Cheirodon terrabae* Bussing as "close to" *C. affinis*, but presented no evidence corroborating this hypothesis. They made a traditional assessment of the number of characters in common between these species but did not explicitly search for derived characters shared by them. This practice has been (and remains) the predominant method of assessing species relationships in ichthyology. It is a process which is logically flawed, and it does not necessarily lead to a stable classification.

To present a broad evaluation of the classification of neotropical characids as expressed in the current literature we must discuss the approach taken by Géry to characid systematics in a long series of papers (see bibliographies in Géry, 1972 and 1977). Géry has been the main proponent in recent years of the "classical" or "Eigenmann" system and much of his work has been recently summarized (Géry, 1977). Because of his efforts to preserve this system Géry has been forced into decisions which, to us, do not make good systematic sense. We cite the following two examples to illustrate the difficulties he encountered and to provide some insight into his rationale and the problems for characid classification that result.

Géry (1966b: 111–112) discussed population samples of a characid which were extremely similar to *Hemigrammus unilineatus* (Gill), a widespread and somewhat variable species of northern South America. In these population samples, all specimens examined had complete lateral lines rather than the reduced ("incomplete") lateral line of *H. unilineatus*, thus giving them the diagnostic feature of another genus, *Moenkhausia*. In his remarks on the situation Géry (1966: 111) stated: "We are thus faced with a form which differs from *H. unilineatus cayennensis*: (a) at the subspecific level (scarcely at the specific one) by a number of characters, and (b) at the generic level by one character, the completeness of the lateral line . . . . The validity of the genus *Moenkhausia* . . . may even be questioned, if the present form is considered as a mere variety of *H. unilineatus*." Near the end of his discussion (p. 112) he stated: "The stability of the nomenclature of Characids [sic] therefore demands that the form here described as *Moenkhausia hemmigramoides* be considered as generically distinct from *Hemigrammus unilineatus*, even though the latter is probably derived from it by regression . . . . Needless to say, this is a compromise." Another example of Géry's systematic practice involves the work of Rosen (1972) on *Bramocharax*, cited above. In spite of Rosen's analysis of relationships of *Bramocharax* species and *Astyanax*, Géry (1977: 302 and 322) chose to recognize *Bramocharax* as a separate tribe, Bramocharacini, placing it "near" the tribe Acestrorhynchini, in the subfamily Characinae rather than in his Tetragonopterinae with *Astyanax*. Géry apparently wished to ignore the documented relationships of *Bramocharax* and stated (p. 302): "Between the two groups [Géry's Characini and Acestrorhynchini], or forming a linking ring with the Tetragonopterinae, is a curious fish, *Bramocharax* . . . in a separate tribe. It resembles an *Astyanax* but with a large characine type mouth and caniniform teeth (as well as pleuricuspid ones)." Géry's concepts of "relationship" clearly are not genealogical and his reference to a "linking ring" is a peculiar echo of the various quinarian taxonomic systems of the early 19th century.

We find Géry's taxonomy to be unac-

ceptable. It is difficult to criticize Géry's work on the basis of a definitive approach to systematics because we are not sure of the nature of his goals and methods. Indeed, Géry has remarked to us personally that his work is not to be taken as an expression of phylogenetic relationships. We certainly agree with him on this point. The difficulty remains that in his papers Géry seems to be writing about relationships based on evolutionary descent, but the meaning of his statements about relationships escapes us. We consider that the price Géry is paying to preserve a traditional system is too high. Efforts to preserve a system which neither represents knowledge of phylogenetic relationships nor acts as a "sorting system," but which instead produces a proliferation of subjective, unsubstantiated judgments about some kinds of undefined "relationships" are counterproductive to efforts to provide a heuristic system for other comparative biologists.

We believe that a new analysis of characid systematics is necessary, one that holds a better promise of eventual systematic stability or which at least clearly defines the problems in any given taxon. For this purpose the phylogenetic approach seems equaled by no others (Farris, 1978; Eldredge, 1979; Wiley, 1981). Characiform phylogenetic analyses have already begun (Vari, 1979; Winterbottom, 1980; Fink and Fink, 1981), but efforts directed toward the American characiforms have so far been limited to Rosen (1972), Weitzman and Cruz (1981), Weitzman and Géry (1981), Vari (1982), Weitzman and Weitzman (1982), and Vari (1983).

A recurrent theme that appears in systematic works on neotropical characids is the difficulty of assessing relationships in the face of specializations accompanying small body size. Many of the "generic" characters discussed above (e.g., incompleteness of the lateral line, reduced caudal-fin squamation) are suspected of having appeared independently in numerous lineages. Myers (1958: 29) noted that a number of reductive evolutionary trends occur in the morphology of small characiforms (and many other small teleosts) with adult body lengths ranging from 10 to 25 mm. Myers attributed these trends to "neoteny." Weitzman (1962: 5–6) also discussed reductive evolution in characids, specifically with reference to osteological features. He warned that "loss of various parts of the laterosensory system, or parts of the skeleton, although providing good characters for identification, must be used with extreme care in the study of phyletic relationships of small fishes, since parallel loss is probably the rule rather than the exception." As noted by Fink (1982) such multiple evolutionary "reductions" amount to anomalies in character distributions in the context of cladograms, usually attributed to paedomorphosis. However, providing a process "explanation" to account for the phenomenon does not change the problems of how such traits may be used in phylogenetic analyses.

The fundamental issue is detecting single *vs.* multiple acquisition of similar morphologies, i.e., detection of synapomorphy *vs.* homoplasy. The only solution to the problem of which we are aware is detection of more derived characters which are congruent with the distribution of certain others, thus providing a basis for choice among competing hypotheses of relationships. Simply because certain traits are "reductive" does not mitigate their usefulness as part of a phylogenetic analysis. Nevertheless, it is wise to look at "reductive" characters very closely, especially when the data are contradictory. In some cases, several aspects of an organism's morphology may be modified by a single change in developmental timing. Hence, all these aspects could be considered a single character rather than several. Comparisons of developmental stages in the taxa where heterochrony is suspected with similar stages in appropriate outgroups often will allow one to determine whether or not, and to what extent, several traits may be "correlated." As will be evident

in the present analysis, the greatest difficulty with this kind of analysis of characids is the lack of well-defined outgroups. For further discussion of models for analysis of ontogenetic processes, see Fink (1982).

IMPLICATIONS OF A PHYLOGENETIC CLASSIFICATION OF THE CHARACIFORMES

In a phylogenetic classification, the groups given names are based on shared derived characters and represent the most parsimonious arrangement of all the attributes of the organisms. In addition, a phylogenetic classification recognizes only complete sets of organisms and their complete subsets, which should represent monophyletic evolutionary lineages. In contrast, a phenetic or traditional "evolutionary" classification recognizes paraphyletic "groups" nomenclaturally. We emphasize here that paraphyletic groups, as incomplete sets, are neither maximally informative about the distribution of attributes of organisms, nor representative of the reality of phylogenetic evolution. Paraphyletic groups are subjective, artificial products of systematists' minds, as discussed by Fink (1979), among others.

The implications of this approach to the classification of the characid and characiform fishes (as well as all "fishes") are profound. Once our knowledge progresses to the point that we can discern lines of evolution within characiform groups, those lineages will be recognized nomenclaturally. It is highly likely, for example, that the family Characidae (*sensu* Greenwood *et al.*, 1966: 383) is a paraphyletic (or perhaps polyphyletic) assemblage of many lineages of fishes with somewhat similar morphological organization. When the phylogenetic relationships of these lineages become clearer, the Characidae will no doubt have to be substantially redefined to represent that increased knowledge.

On a lower taxonomic level, we cite as an example a genus that was discussed above. *Astyanax* is a large assemblage of "generalized" characid species all of which are supposed to possess a spectrum of "key" characters that "define" the genus. But it is possible, perhaps likely, that there are several independent evolutionary lineages within *Astyanax*, making it a polyphyletic genus. Many species of *Astyanax* may be more closely related to (are the sister group of) species now placed in other genera. As an example of the latter case, we would cite the genus *Bramocharax* of Central America. Rosen (1972: 12–16) considered the possibility of synonymizing *Bramocharax* with *Astyanax*, but retained the former on the basis of at least one unique character. Nevertheless, it is clear from his discussion that the species now placed in *Bramocharax* have as their sister group one or more species of *Astyanax*. Should these sister group relations be delineated by use of the name *Bramocharax*, then *Astyanax* would have to be considered paraphyletic. To retain a phylogenetic classification, either the *Bramocharax* species would have to be placed within *Astyanax* with their relatives, or the related "*Astyanax*" species would have to be placed in *Bramocharax*.

Stated in another way, if "*Astyanax*" ancestors have given rise to autochthonous specialized lineages (like *Bramocharax*) in various geographical areas of South America, then, to maintain a monophyletic classification, the "*Astyanax*" descendants of those ancestors will have to be placed with their specialized relatives, rather than with their more distant "generalized" relatives.

We expect that the classification of the American characids, and indeed of all the characiforms, will be subject to much reinterpretation and rearrangement as a result of phylogenetic analyses. We would also suggest that the Characiformes is only one of many groups in need of such studies. For example, many members of the gobies (Gobiidae, Eleotridae, and their

Figure 1. Adult live *Paracheirodon simulans*, female above, SL 23.9 mm, male below, SL 21.2 mm, USNM 216973.

putative relatives) and cypriniforms (Cyprinidae and related fishes) display features presumably associated with small size. Both groups are currently the subjects of primarily typological classifications and subjective evolutionary systematic approaches. Understanding of their relationships would be greatly enhanced by phylogenetic analyses.

A HISTORY OF THE NEON TETRA PROBLEM

The neon tetras (Figs. 1–3) are three species of small, brilliantly colored freshwater fishes from South America that have come to the attention of ichthyologists through the aquarium trade. Géry (1960b: 9–13 and 1963: 14) assigned each species to a different genus and referred two of the species to one characid subfamily and the third to another as follows: *Hyphessobrycon simulans* Géry, the green neon, was placed in the Tetragonopterinae (Géry, 1963: 70–71), while *Cheirodon axelrodi* Schultz, the cardinal tetra, and *Paracheirodon innesi* (Myers), the neon tetra, were placed in the Cheirodontinae (Géry, 1960b: 9–13). Although the last two species are well known and kept in aquaria by millions of people because of their intense red and green to blue life colors, all three species remain poorly studied by ichthyologists. In our view former hypotheses concerning their relationships can be rejected both by a reevaluation of evidence provided by former authors and by new evidence presented here. We propose that the three "neon tetras" form a monophyletic group, represented by the genus

Figure 2. Adult live *Paracheirodon axelrodi*, male above, SL 28.9 mm, female below, SL 31.1 mm. Specimens not retained.

Paracheirodon.[1] See the species descriptions for new locality records for these three species and a discussion of their distribution.

Myers (1936: 97) described the first known neon tetra, *Paracheirodon innesi*, and placed it in the genus *Hyphessobrycon*, subfamily Tetragonopterinae, because, among other characters, the holotype appeared to have two rows of premaxillary teeth, the "outer row" represented by a single tooth. Schultz (1956: 42) and Myers and Weitzman (1956: 1) nearly simultaneously described a second species, here called *Paracheirodon axelrodi*, with a color pattern similar to the neon tetra. All these authors recognized that *P. axelrodi* had only one row of premaxillary teeth and that it should be placed in the Cheirodontinae according to the then currently accepted subfamilies. Myers and Weitzman chose to question the validity of at least part of the Cheirodontinae because of the apparent relationship of the two species based on color pattern and body shape. Schultz, on the other hand, chose to place the new fish in

[1] The type of the genus *Paracheirodon* (Géry, 1960b: 12) is *Hyphessobrycon innesi* Myers (1936) and the name is available for application to all of the neon tetras. Another name, *Lamprocheirodon* Géry (1960b: 13), proposed as a subgenus with *Cheirodon axelrodi* Schultz (1956) as its type, is also available for the three species, but *Paracheirodon* has line precedence over *Lamprocheirodon*.

Figure 3. Adult live *Paracheirodon innesi*, female above, SL 25.1 mm, male below, SL 26.9 mm. Specimens not retained.

Cheirodon, where it "fit" because of its single premaxillary tooth row, thus not upsetting Eigenmann's system.

Géry (1960b: 9–13) examined the relationships of the two neon tetras (then called *Hyphessobrycon innesi* and *Cheirodon axelrodi*) to each other and to other small characids, especially those with one row of premaxillary teeth, grouped as the Cheirodontinae. Géry's analysis is useful, and although to a large extent based on the concepts of generic relationships for the Cheirodontinae published by Eigenmann (1915: 14–17), it includes several hypotheses of possible importance in any study of the phylogeny of small characiforms. Unfortunately, his study was marred by many errors of morphological interpretation (see discussion below on uninformative characters). Géry's work also displays a few interpretive contradictions that in some places made the relationships he proposed unclear.

Because Géry's paper was an attempt to elucidate the "relationships" of many "cheirodontins," including the two neon tetras mentioned above, a review of his basic hypotheses is in order. Géry (1960b: 2–5) proposed to divide the genera of the entire subfamily into two basic groups, the first (divided by Géry at that time into three subgroups) having tricuspid or unicuspid teeth and the second having five or more cusps (*Cheirodon* and seemingly related genera). This was done despite the fact that one species of the second group,

Cheirodon australis Eigenmann, from Chile, was known to have tricuspid teeth. Subsequently Géry (1973: 81) divided the group with unicuspid or tricuspid teeth into two groups (instead of the three in Géry, 1960b: 2–5), those with mostly unicuspid teeth, the Aphyoditeina, and those having tricuspid teeth, left unnamed. As with the Cheirodontinae itself, we think that these subgroups, as currently proposed, will ultimately be rejected. Géry himself (1960a: 32–34 and b: 1–5, 1973: 81) expressed reservations about the validity of the groups.

Géry (1960b: 5–9) proposed five groups in the genus *Cheirodon*. The first two groups included three or four nominal species, including the type of the genus, *Cheirodon pisciculus* Girard, from the west side of the Andean Cordillera in Peru and Chile. The next two groups are found primarily on the eastern side of the Andes and northward into Central America. Eigenmann (1915: 64) was also aware of this possible division into groups east and west of the Andes, and we concur that this suggested separation is worthy of a detailed investigation, even though, as Géry (1960b: 6) suggested, there appear to be "intermediate" species. Géry's fifth group (1960b: 8) is represented by only *Paracheirodon axelrodi*. Géry (1960b: 9–13) was unsure of the relationships of *P. innesi* but believed that since it did not have teeth with five or more cusps, it could not be a *Cheirodon*.

Of primary interest to us here are those groups proposed by Géry (1960b and 1963) to be related to the neon tetras. Géry (1960b: 8–9) suggested that *P. axelrodi* was "nearer to the type" of *Cheirodon* (*C. pisciculus*) or to *Cheirodon stenodon* Eigenmann than to the small, deep-bodied species occurring mostly east of the Andean Cordillera such as *Cheirodon interruptus* (Jenyns). Géry (1960b: 9) stated that *P. axelrodi* shows similarities to *Myxobrycon* Eigenmann but noted at least one major difference from the latter, poorly known, genus. He then stated that *P. axelrodi* "may be close" to *Pseudocheirodon* Meek and Hildebrand. Fink and Weitzman (1974: 3–5) placed *Pseudocheirodon* as a synonym of *Cheirodon*, noting its close similarity with the groups of *Cheirodon* species east of the Andes. Thus, Géry (1960b: 8–9) proposed that *P. axelrodi* is most closely related to the species west of the Andean mountains but also stated that it is perhaps closely related to a genus and species now placed with the species of *Cheirodon* found to the east of the Andes.

Of the relationships of *Paracheirodon innesi*, Géry (1960b: 9) stated that it ". . . has striking morphological affinities with *Cheirodon* [he does not mention at this point which group of *Cheirodon*, those to the east or those to the west of the Andean mountains], but some structures (in particular the teeth) make it more probably intermediate between the first and second groups of 'tricuspid Cheirodontinae,' being perhaps the link between *Megalamphodus* (for example) and *Cheirodon* (for example)." The genera in Géry's first "tricuspid group" were *Megalamphodus* Eigenmann, *Pristella* Eigenmann, *Pseudopristella* Géry, and *Oligobrycon* Eigenmann. His second "tricuspid group" included *Prodontocharax* Eigenmann and Pearson, *Microschemobrycon* Eigenmann, *Aphyocharacidium* Géry, and *Aphyocheirodon* Eigenmann; it did not include *Cheirodon*, which, as noted above, was grouped with other genera characterized by teeth with five or more cusps. Thus, Géry seemed to say two, contradictory things: first, that *P. innesi* is intermediate between two groups of "cheirodontins" with tricuspid teeth and second, that it is a "link" between *Megalamphodus*, which belongs to one of those groups, and *Cheirodon*, which Géry placed in a group separate from the "tricuspid teeth group."

After apparently disassociating *P. innesi* and *P. axelrodi* in the above manner, Géry (1960b: 13) raised another possibility, stating that although *P. innesi* is "an-

atomically rather near to *Megalamphodus* or *Oligobrycon* (seeming intermediate between the two already mentioned groups)," it is "also near to a third group represented by the aberrant *Cheirodon axelrodi* (by a remarkable evolutive [sic] convergency or, more probably, by a real phylogenetic affinity)." The evidence Géry used to support his views will be discussed below, but our interpretation of the characters is very different from his.

Géry's understandable indecision and apparent confusion regarding the relationships of the neon tetras may be alluded to by quoting the following statement made by him later (1963: 13) regarding his earlier study (1960b) of these two species. After noting that the two neon tetras, *P. axelrodi* and *P. innesi*, ". . . have unusual skull, jaws and teeth structures," he stated the following: "These peculiarities place them in 'border-groups,' in boundaries between the tetragonopterins on the one hand, and the cheirodontins on the other. Their existence, together with that of several other forms seems even to show that the last named groups are quite artificial and may be united in a natural classification. It was also suggested that, although being technically in different (but very close) genera, both species may have arisen from a common stem. Otherwise their remarkable convergency (same habits and coloration) could not satisfactorily be explained."

Géry (1960b: 1) noted that the above two species had been hybridized by an aquarist. Unfortunately the results of this are unknown to us and apparently have never been published.

In his description of the third neon tetra, *P. simulans*, Géry (1963: 70–71) stated the following: "It is indeed a genuine *Hyphessobrycon* with two well separated rows of teeth on the premaxillary and an elongate pedicel [ascending premaxillary process]." In a footnote, Géry noted that the genus *Hyphessobrycon* perhaps should be split into two genera. Géry did not relate *P. simulans* to any known species of *Hyphessobrycon* and stated that ". . . none seems to be very close to *H. simulans*." Géry (1963: 71) further stated that *P. simulans* has a color pattern similar to that of *P. innesi* and that he believed such a color pattern similarity to be due to convergence. He noted several morphological differences between *P. simulans* and the other two neon tetras in support of this hypothesis.

More recently, Géry suggested yet another possibility regarding the relationship of *P. innesi*. In regard to his studies on the "Aphyoditeina," Géry (1973: 81) noted that the possible relationship of *P. innesi* to the "Aphyoditeina" needs to be considered.

It is difficult to summarize Géry's views about the relationships of the three neon tetras. As noted above, he continued to place them in three different genera, with *Paracheirodon innesi* and *Cheirodon axelrodi* in one subfamily, the Cheirodontinae, and *Hyphessobrycon simulans* in the Tetragonopterinae. He appeared to believe that *P. innesi* and *P. axelrodi* must be related in some way even though possessing "technical" characters that "required" their placement in separate genera and separate sections of the Cheirodontinae. He also stated that these two species belong in "borderline" cheirodontine groups, near the Tetragonopterinae, but suggested (Géry, 1963: 71) that *Hyphessobrycon simulans* acquired its "neon" color pattern independently of *P. innesi* and *P. axelrodi*.

Another hypothesis regarding the relationships of these fishes has been proposed by Scheel and Christensen (1970) and Scheel (1972), who studied the chromosomes of these small characids. They proposed that *P. innesi* and *P. axelrodi* are ". . . distantly related, the similarities [sic] colors reflecting convergence and not close relationships" (Scheel and Christensen, 1970: 31) and that *P. simulans* ". . . is karyotypically much closer to a large number of dissimilar-looking tetras than to the other two neon tetras" (Scheel, 1972:

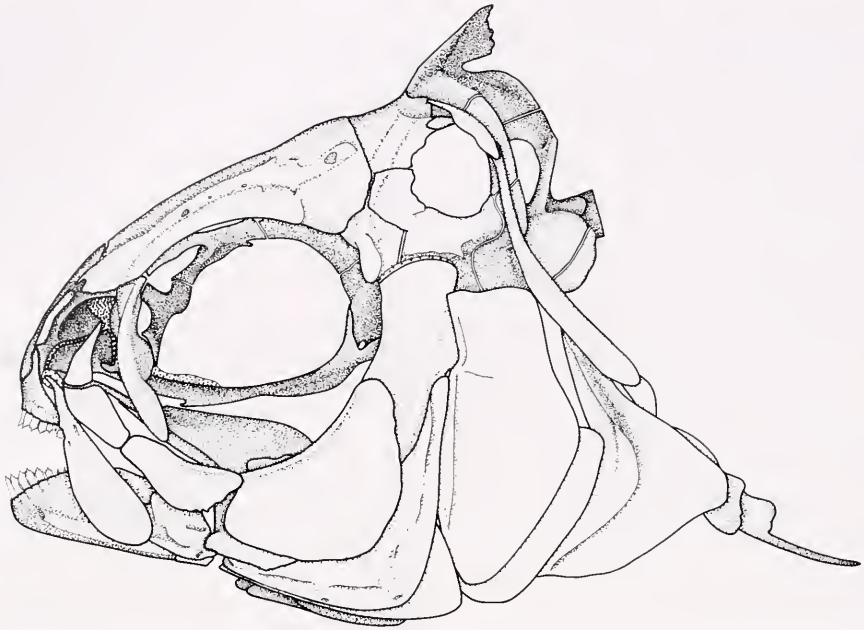

Figure 4. Skull and pectoral girdle of large adult female *Paracheirodon axelrodi*, SL 31.3 mm, USNM 216910, lateral view, left side.

65). These authors' analyses can be faulted for several reasons which are dealt with in more detail below (see discussion on currently uninformative characters). Suffice it to say here that the concept of relationships used appears to be phenetic and there was no attempt by the authors to distinguish derived from primitive similarities in the karyotypes.

In an anonymous introduction to the study of the chromosomes of *P. innesi* and *P. axelrodi* by Scheel and Christensen (1970: 24), the following paraphrased opinion was expressed. To many aquarists the cardinal and neon tetras appear very similar, their most obvious differences being in the extent of the red pigment along the sides of the body. Since the two species also have similar behavior (apparently including breeding behavior) and roughly similar aquarium requirements, a few interested aquarists have concluded that these species are sufficiently alike so that their separate generic placement is of doubtful validity and that they should be placed in one genus. It was then pointed out by the anonymous author that evidence presented by Scheel and Christensen suggested that their similarities are due to convergence. Our own analysis indicates that the aquarists are closer to the truth than most of the various investigators publishing on the subject. One aquarist, Madsen (1975: 162), was so confident of the seemingly obvious relationship between *P. simulans* and *P. axelrodi* that he placed both species in the genus *Cheirodon*. Another author, Van Ramshorst (1981: 142), placed *P. innesi* in *Cheirodon*.

Although we have found synapomorphies that indicate a relationship among the three species of *Paracheirodon* as defined below, we have been unable to formulate a hypothesis of their relationship to any other specific characid group. In

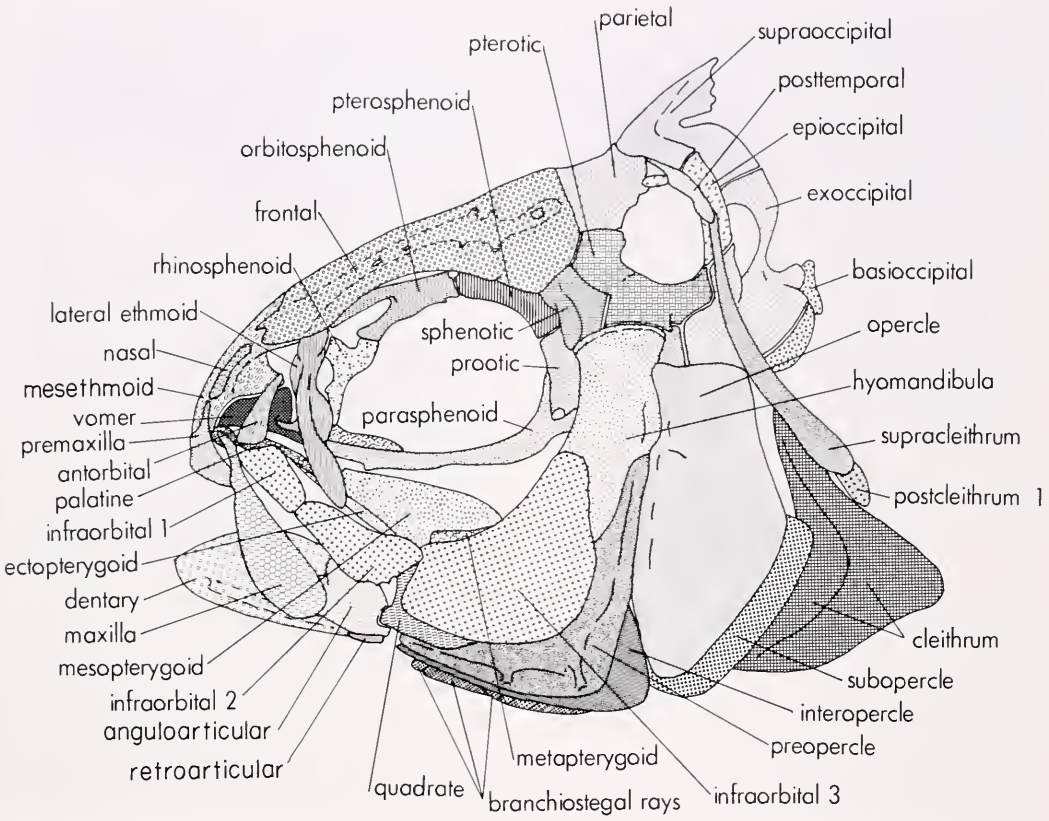

Figure 5. Diagram of skull and pectoral girdle of *Paracheirodon axelrodi* with each bone represented by a different pattern. Adult female, SL 31.3 mm, USNM 216910, lateral view, left side.

part this may be due to the poor morphological information available for possibly related characid groups. Before forming hypotheses of relationship among the various groups of small and miniature characids, those groups need to be diagnosed by further phylogenetic studies. The present contribution is only a beginning attempt to identify monophyletic characid groups.

Paracheirodon Géry

Paracheirodon Géry, 1960b: 12 (type species: *Hyphessobrycon innesi* Myers, by original designation).

Lamprocheirodon Géry, 1960b: 13, as a subgenus (type species: *Cheirodon axelrodi* Schultz, by original designation).

PHYLOGENETIC ANALYSIS OF *PARACHEIRODON*

Below we present evidence for the monophyly of *Paracheirodon*. For each character, the derived state is listed first, followed by the character as found in outgroups.

In the skull figures we use a diagrammatic representation with a standardized pattern for each bone. The skull of *P. axelrodi*, unlabeled in Figure 4, is repeated and labeled in pattern form in Figure 5. These two figures are provided in part as a guide to the use of the remaining skull figures.

The following characters are synapomorphies for the neon tetras.

1) In life there is an intense blue or blue-green lateral body stripe. In other characids, a lateral body stripe is common, most often silvery, or also reddish, red orange, and pale green, but never of the intensity found in *Paracheirodon*.

2) In life dense red pigment is restricted to the region ventral to the lateral stripe. All other American characids in which live pigmentation is known lack the dense pigment of this pattern. Géry (1966a: 116) stated that in freshly preserved *Axelrodia riesei* ". . . the fish is almost entirely of the same red color as that of the cardinal tetra, *Cheirodon axelrodi*; only the belly and lower part of the head are plain; . . ." The distribution of the red pigment of *A. riesei* over most of the body as described by Géry is different from that of *Paracheirodon*. Further, we suspect that the intensity of the color in Géry's specimens of *Axelrodia* can be attributed to fixation artifact caused by formalin. Many small characids with silvery or white abdominal pigment, when fixed in formalin, develop a pink or even red abdominal region. A photograph of *Axelrodia riesei* in life (Géry, 1966a: 111, Fig. 1) shows much less red than the preserved specimen. We know of no other species of American characids whose pigmentation can be compared to that of the *Paracheirodon* species.

The red pigmentation extends well anterior to the pelvic fins in *P. axelrodi* and *P. simulans*. In *P. innesi* the red pigment does not extend to the pelvic-fin base. Lack of a precise outgroup prevents our use of this pigment distribution for phylogenetic evaluation within *Paracheirodon*.

3) A stripe of dark brown or black chromatophores underlies and extends dorsal to the blue lateral stripe. In other characids with a colored lateral stripe the underlying dark chromatophores, when not restricted to the immediate area of the colored stripe, lie ventral to the colored stripe rather than dorsal to it.

4) The pterotic aponeurosis is attached to the cranium near the middle of the anterolateral border of the posttemporal fossa, where it attaches either to the pterotic or sphenotic bones (Figs. 6–8). In other characids examined (Figs. 9–18) this aponeurosis extends from a spinous process of the pterotic bone located at the ventral border of the posttemporal fossa. The pterotic aponeurosis is attached posteriorly to epaxial body musculature in all cases.

5) The joint between the posttemporal and supracleithrum is placed at or dorsal to the midpoint of the vertical length of the posterior border of the posttemporal fossa (Figs. 6–8). In other characids examined (Figs. 9–18) the joint lies at or ventral to the ventral border of the posttemporal fossa.

6) The epioccipital bridge (very reduced and occasionally absent in some specimens of *P. simulans*, Fig. 6) lies at the dorsal border of the posttemporal fossa (Figs. 7, 8). It bisects the fossa in its mid-region or lies just dorsal to it in most characids (Figs. 9–11). In *Hemigrammus erythrozonus* (Fig. 12), *Axelrodia riesei* (Fig. 13), *Brittanichthys axelrodi* (Fig. 14), *Characidium* sp. (Fig. 16), and *Elachocharax geryi* (Fig. 18) the bridge, or parts of it, are placed dorsally but never as far as in the species of *Paracheirodon*. In some characids the epioccipital bridge is absent (Fig. 15 of *Tyttocharax madeirae*, a glandulocaudine, and Fig. 17 of *Klausewitzia aphanes*, a characidiinin). This absence of an epioccipital bridge is most parsimoniously interpreted as independently lost in these two "subfamilies" and in *Paracheirodon simulans*.

7) The ventral posttemporal ligament extends between the ventral arm or process of the posttemporal bone and the intercalar. The latter is located on the lateral surface of that part of the pterotic bone which bears the horizontal semicircular canal. In other characids examined the intercalar and its attached ligament are placed at or very near to the common joint area of the pterotic, exoccipital, and the basioccipital.

8) The dorsal profile of the parietal bone

Figure 6. Postocular skull region and dorsal part of pectoral girdle of *Paracheirodon simulans*, adult female, SL 23.9 mm, USNM 216738, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

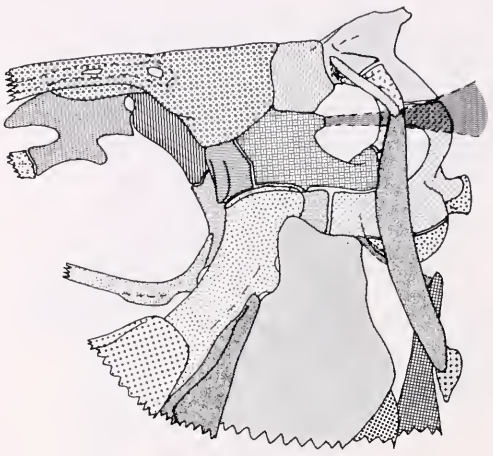

Figure 8. Postocular skull region and dorsal part of pectoral girdle of *Paracheirodon innesi*, adult female, SL 24.6 mm, USNM 216912, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

is flat or concaved in lateral view and the supraoccipital projects dorsally from the posterior border of the parietal (Figs. 6–8). This character is evident in the "pinched nape" look seen in Figures 1 to 3 of live specimens. In other relatively slender characids examined with a relatively elongate body shape, the dorsal profile of the posterior region of the skull is approximately straight (Figs. 9, 11–18). In

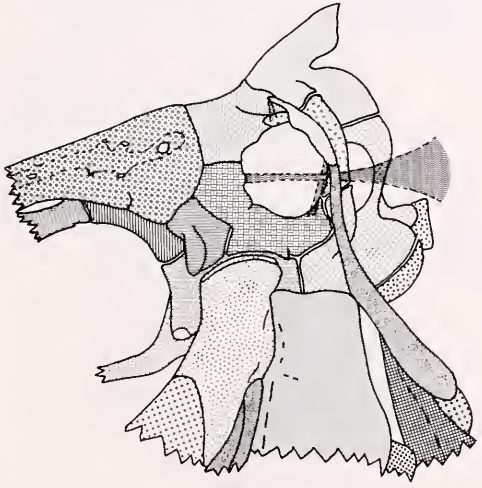

Figure 7. Postocular skull region and dorsal part of pectoral girdle of *Paracheirodon axelrodi*, adult female, SL 31.3 mm, USNM 216910, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

Figure 9. Posterior region of skull and pectoral girdle of *Astyanax fasciatus mexicanus*, female, SL 52.4 mm, MCZ 41365, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

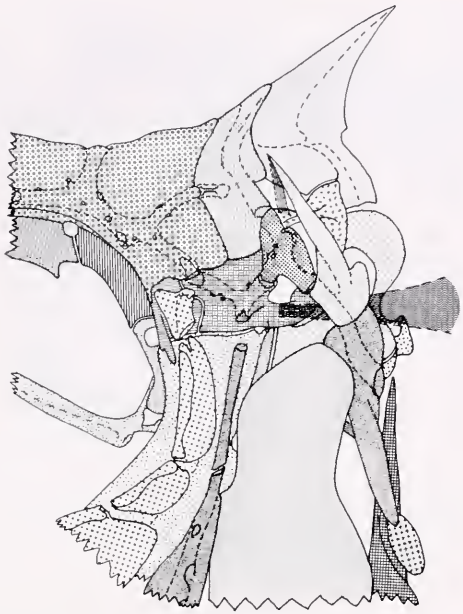

Figure 10. Postocular region of skull and pectoral girdle of *Gymnocorymbus thayeri*, adult, SL 27.5 mm, CAS(IUM) 15881, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

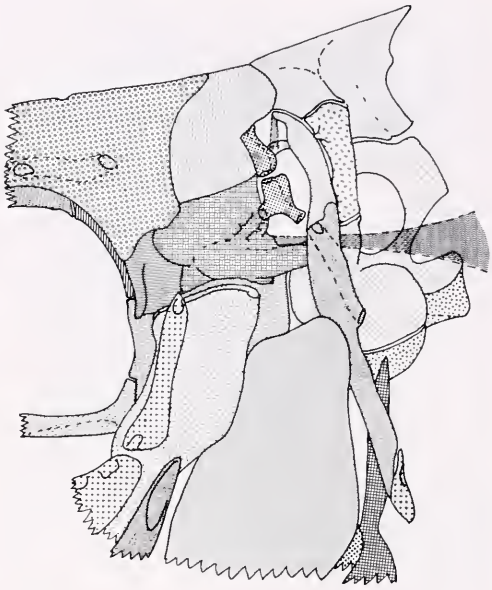

Figure 12. Postocular region of skull and pectoral girdle of *Hemigrammus erythrozonus*, adult male, SL 24.2 mm, USNM 216709, lateral view, left side. Note: Extrascapular of contralateral side is a single bone.

Key to Patterns: See Figure 5, p. 351.

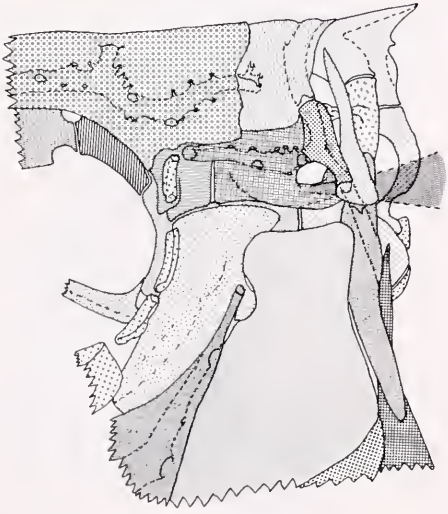

Figure 11. Postocular region of skull and pectoral girdle of *Cheirodon interruptus*, adult female, SL 27.0 mm, FMNH 50629, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

Figure 13. Postocular region of skull and pectoral girdle of *Axelrodia riesei*, SL 16.2 mm, USNM 221681, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

Figure 14. Postocular region of skull and pectoral girdle of *Brittanichthys axelrodi,* adult female, SL 22.2 mm, USNM 221682, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

deep-bodied characids such as *Gymnocorymbus thayeri* (Fig. 10), the entire dorsal profile from anterior to the epiphyseal bar of the frontal bone and the posterodorsal apex of the supraoccipital spine

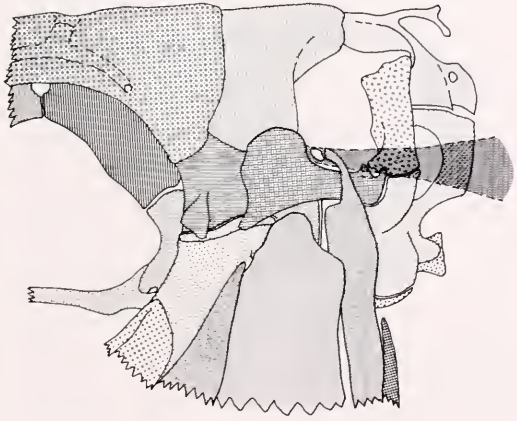

Figure 15. Postocular region of skull and pectoral girdle of *Tyttocharax madeirae,* adult male, SL 17.9 mm, USNM 222007, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

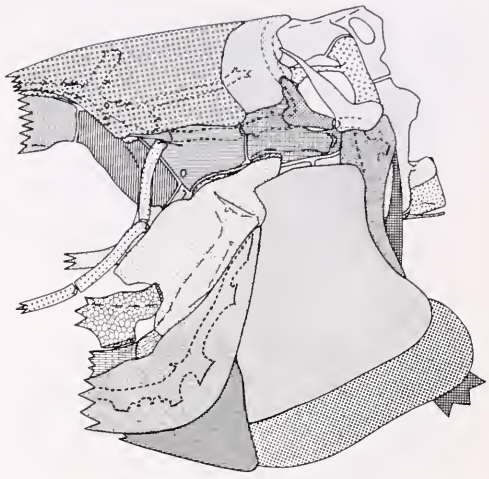

Figure 16. Postocular region of skull and pectoral girdle of *Characidium* sp., adult, SL 35.0 mm, USNM 222017, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

is concave, with the parietal and supraoccipital curving dorsally.

KEY TO SPECIES OF *PARACHEIRODON*

1a. Premaxilla with teeth in 2 distinct rows (Fig. 19A–E); outer row of 1 or sometimes 2 conical teeth; inner row of 4–5 multicuspid teeth with 5–9 cusps; maxilla usually toothless, sometimes with 1 conical tooth; dorsal fin with 7–8, usually 8, branched rays; pectoral fin with 7–9, usually 8, branched rays; pelvic fin with 5–6, usually 6, branched rays; blue-green stripe on body sides of live specimens posteriorly terminating at caudal-fin base ..... *Paracheirodon simulans*

1b. Premaxilla with teeth in 1 row or with 1 row having 1 or 2 teeth somewhat offset anteriorly at their bases (Fig. 20A–D, Fig. 21A–E, Fig. 22A–C) [sometimes aged aquarium specimens will have abnormal teeth in two irregular rows (Fig. 23A–D)]; premaxillary tooth row with 5 teeth, each with 5 cusps (specimens less than 10 mm SL with 3 cusps) or with 6–7 teeth, each with 3 cusps; maxilla with 1 tooth having 3–5 cusps or 2–3 teeth having 3 cusps; dorsal fin with 8–9, almost always 9, branched rays; pectoral fin with 10–13, usually 10–12, branched rays; pelvic fin with 7, rarely 6, branched rays; blue-green stripe on body sides of live specimens pos-

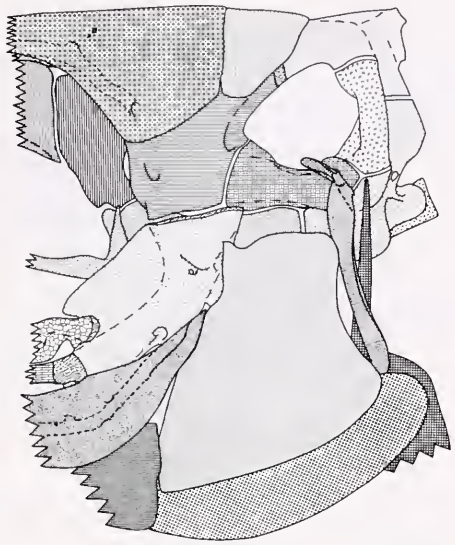

Figure 17. Postocular region of skull and pectoral girdle of *Klausewitzia aphanes,* adult, SL 14.9 mm, USNM 221995, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

teriorly terminating near adipose-fin base, not reaching caudal-fin base 2

2a. Premaxilla with 1 row of 5 teeth each having 5 cusps (3 cusps in specimens of less than 10 mm SL) (Fig. 20A–D); maxilla with 1 tooth with 5 cusps; dentary with anterior teeth often having 5, but up to 7 cusps; ventral-limb gill rakers 12–14, usually 12–13; perforated lateral-line scales 5–8, usually 6–7; red pigment on body sides of live specimens extending well anterior to pelvic-fin base ..... *Paracheirodon axelrodi*

2b. Premaxilla with 1 row of 6–7, rarely 8, teeth each having no more than 3 cusps (Fig. 21A–E, Fig. 22A–C); often 1 or sometimes 2 of these teeth offset anteriorly at their bases giving appearance of 2 rows unless flesh is cleared to base of teeth where their approximation to 1 row can be seen (Fig. 21A,B); maxilla with 2–3 teeth, each with no more than 3 cusps (Fig. 21C,D); each dentary tooth with no more than 3 cusps (Fig. 21F); ventral-limb gill rakers 10–11, usually 11; perforated lateral-line scales 3–6, usually 4–5; red pigment on body sides of live specimens not extending anterior to pelvic-fin base ..... *Paracheirodon innesi*

Figure 18. Postocular region of skull and pectoral girdle of *Elachocharax geryi,* small adult, SL 12.5 mm, USNM 215288, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

Paracheirodon simulans (Géry)
Figures 1, 6, 19C, 24C, 25; Tables 1, 4 to 7

Hyphessobrycon simulans Géry, 1963: 15, original description, Brazil, "in the Rio Purus" (see discussion, Appendix 2).—Géry, 1966c: 231, correction of type locality.—Scheel, 1972: 60, relationships based on chromosomes.—Géry, 1977: 474, 563, 587, relationships.

Cheirodon simulans (Géry), Madsen, 1975: 162, aquarium description, referral of *P. simulans* to *Cheirodon.*

Specimens Examined. 1, paratype, USNM 197510, SL 16.1 mm, Brazil, Amazonas, Rio Jufari (=Tupari) 1°15′S, 62°0′W), tributary to Rio Negro near mouth of Rio Branco, November 1962, H. W. Schwartz [Note: original type locality listed by Géry (1963) as "lower Rio Purus," Amazonas, Brazil was corrected to that given above by Géry (1966c)].—12, USNM 216896, SL 12.0–13.3 mm, Venezuela, Amazonas, caño tributary to Río Orinoco approximately 14 km east of San Fernando de Atabapo (4°4′N, 67°42′W), 14 April 1972, Alvaro Cortez.—Following lots with same locality information as USNM 216896 preceeding: 11, MBUCV-V 7283, SL 10.4–14.2 mm; 12, ANSP 138020, SL 10.3–13.7 mm; 3 alizarin preparations, USNM 216915, SL 12.5–14.6 mm.—1, MBUCV-V 7471, SL 17.8 mm, Venezuela, Amazonas, caño 20 km east of San Fernando de Atabapo (4°4′N, 67°42′W) towards Santa Bárbara, 13 April 1972, Alvaro Cortez.—3, USNM 216750, SL 13.1–15.0 mm and 3,

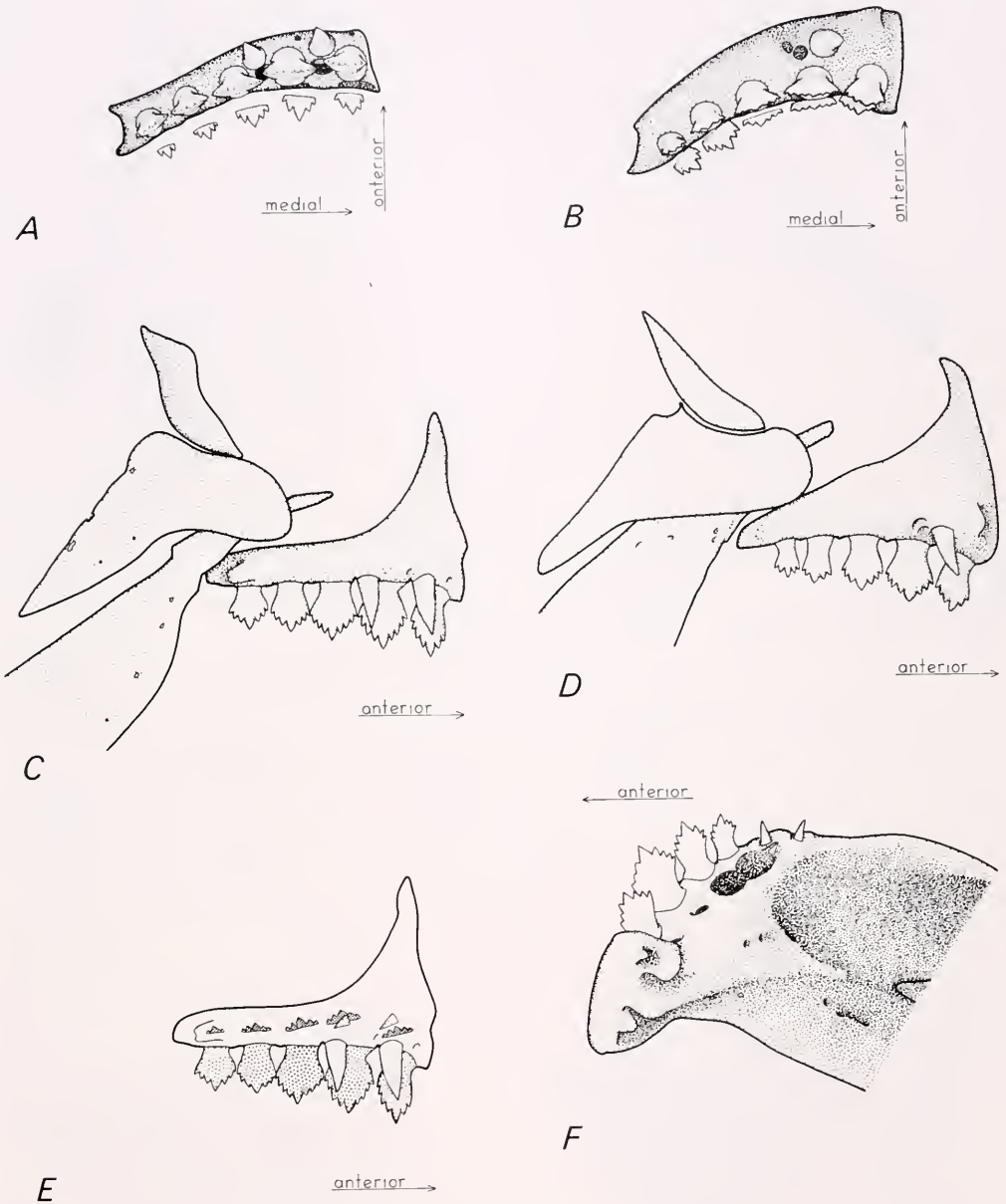

Figure 19. Teeth and jaws of *Paracheirodon simulans*. A. Premaxilla, ventral view, right side of adult SL 20.0 mm, USNM 216913. B. Premaxilla, ventral view, right side of large adult, SL 23.9 mm, USNM 216913. C. Premaxilla, maxilla, infraorbital 1, antorbital, and reduced nasal bone, anterolateral view, right side of adult, SL 20.0 mm, USNM 216913. D. Same series of bones as in C. preceeding (nasal bone absent), anterolateral view, large adult, SL 23.9 mm, USNM 216913. E. Transparency of premaxilla, anterolateral view of adult, SL 20.0 mm, USNM 216913, showing position of replacement teeth within bone. F. Dentary, medial view, right side of large adult, SL 23.9 mm, USNM 216913.

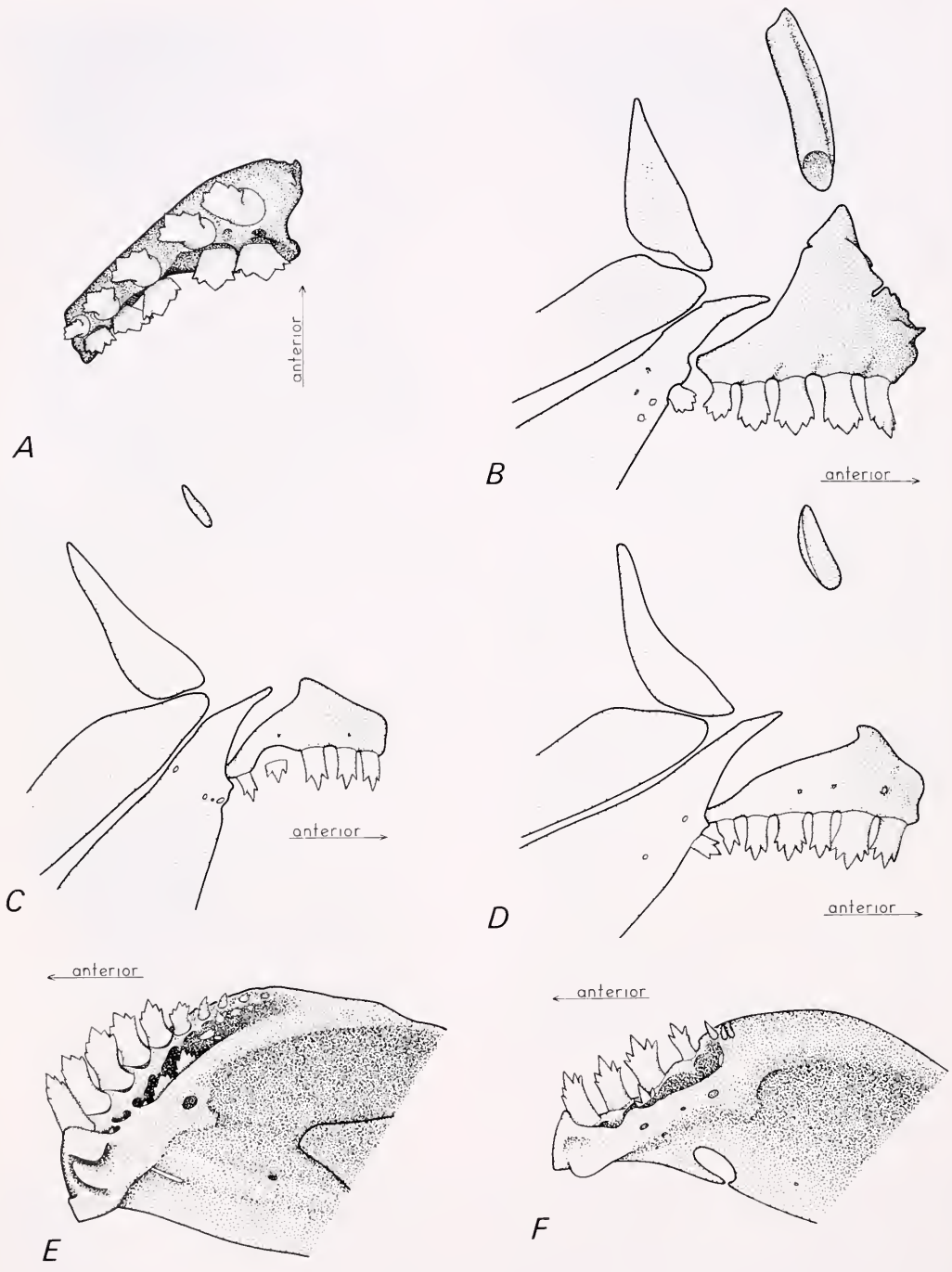

Figure 20. Teeth and jaws of *Paracheirodon axelrodi*. A. Premaxilla, ventral view, right side of large adult, SL 33.1 mm, USNM 216910. Nearly fully developed replacement teeth posterior to teeth ankylosed to jaw produce appearance of two tooth rows. B. Premaxilla, maxilla, infraorbital 1, antorbital, and nasal bones in anterolateral view, right side of large adult, SL 33.1 mm, USNM 216910. C. Same series of bones as in B. preceeding, anterolateral view, right side of juvenile, SL 10.1 mm, MCZ 52459. D. Same series of bones as in B. preceeding, anterolateral view, right side of juvenile, SL 11.9 mm, MCZ 52459. E. Dentary, medial view, right side of large adult, SL 33.1 mm, USNM 216910. F. Dentary, medial view, right side of juvenile, SL 10.1 mm, MCZ 52459.

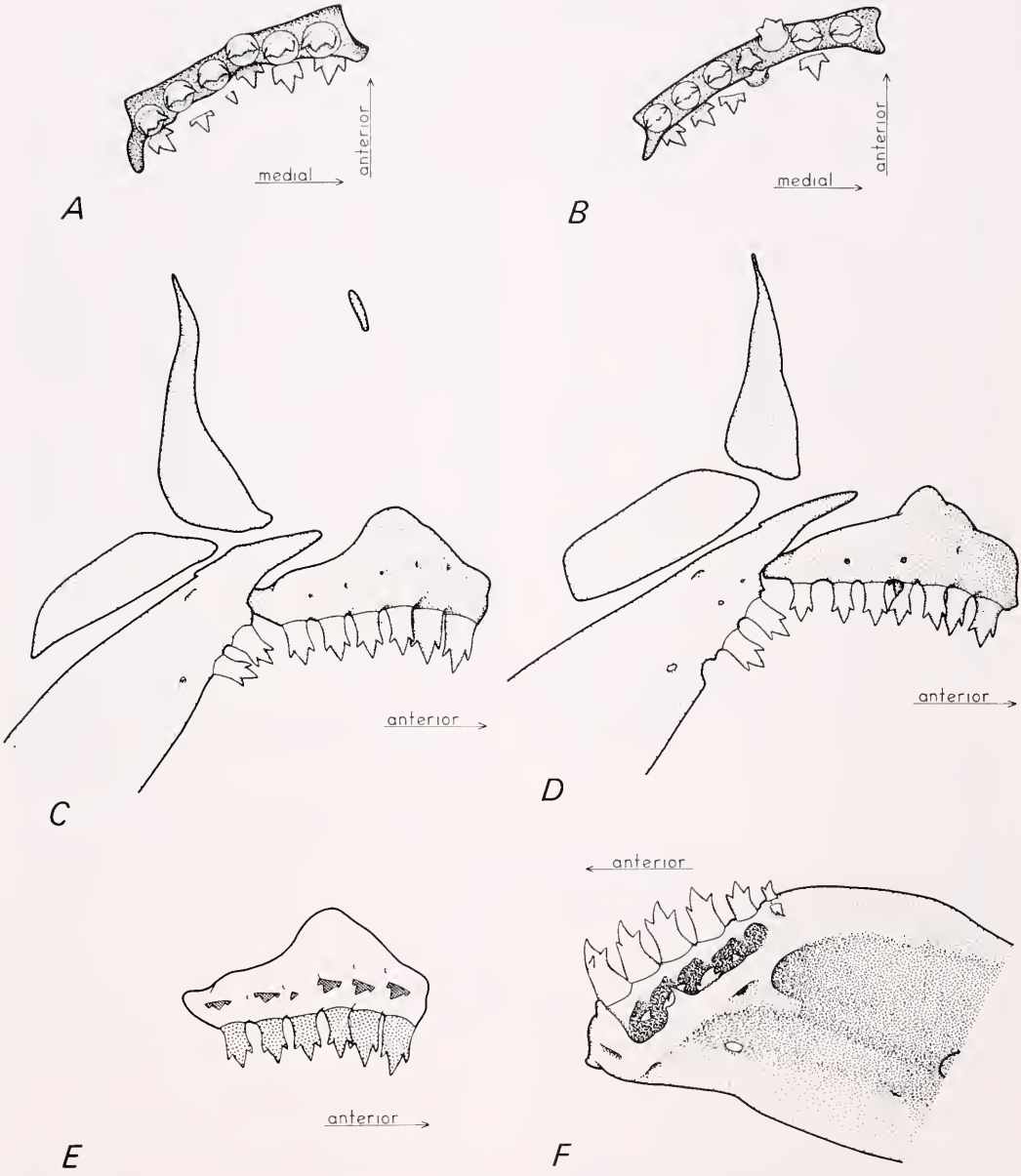

Figure 21. Teeth and jaws of *Paracheirodon innesi*. A. Premaxilla, ventral view, right side of adult, SL 21.5 mm, USNM 216912. B. Premaxilla, ventral view, right side of adult, SL 21.8 mm, USNM 216912. C. Premaxilla, maxilla, infraorbital 1, antorbital, and nasal of adult, anterolateral view, right side, adult, SL 21.5 mm, USNM 216912. D. Same series of bones as in C. preceeding, anterolateral side of adult, SL 21.8 mm, USNM 216912. E. Transparency of premaxilla, anterolateral view of adult, SL 21.5 mm, USNM 216912, showing position of replacement teeth within bone. F. Dentary, medial view, right side of adult, SL 21.5 mm, USNM 216912.

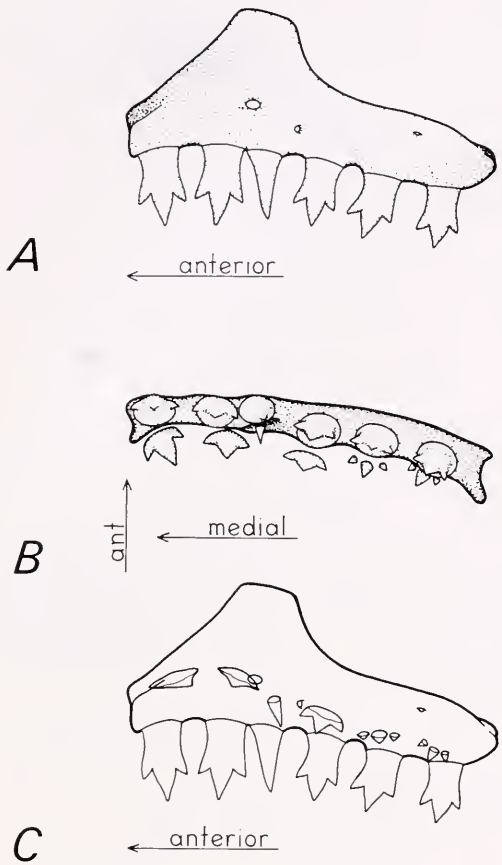

Figure 22. Premaxillary bone of *Paracheirodon innesi* juvenile, SL 13.5 mm, MCZ 52156. A. Anterior view, left side. B. Ventral view, left side. C. Anterior view, left side; bone shown as transparent so that position of replacement teeth may be seen.

MBUCV-V 8653, Venezuela, Amazonas, upper Rio Orinoco, affluent of Caño Cadabaudi at Esmeralda (3°11'N, 65°34'W), 25 January 1969, Francisco Mago-Leccia, Jose Mosco, Antonio Machado.—Following specimens all collected for aquarium trade, some with at least modestly helpful locality information: 13, USNM 216737, SL 10.1–19.6 mm, Colombia, Vichada, collected "out of Puerto Correño" (6°12'N, 67°30'W) at mouth of Río Meta into Río Orinoco, July–September 1975 for Capt. E. Siaz. Note: it is very likely that these fishes were collected at various sites south of Puerto Correño, in tributaries of the Río Orinoco in both Colombia and Venezuela.—Following lots have same locality information as USNM 216737 immediately preceeding: 12 alizarin preparations, USNM 216736, SL 9.3–20.3 mm; 7, USNM 216911, SL 11.2–13.5 mm; 10 alizarin preparations, MCZ 52339, SL 10.9–19.5 mm; 4, ANSP 137964, SL 11.5–16.6 mm; 2, BMNH 1977.3.11.5–6, SL 11.9–17.3 mm; 4, MZUSP, SL 10.4–19.1 mm.—5, USNM 216738, SL 17.0–23.5 mm and 4 alizarin preparations, USNM 216913, SL 21.2–23.9 mm, aquarium specimens possibly from same locality as USNM 216737 or from some aquarium collection station on upper Rio Negro in Amazonas, Brazil, 1974 or 1975.

Paracheirodon simulans occurs in the upper Rio Negro region of Brazil from near the mouth of the Rio Branco and in the Río Orinoco in the region of San Fernando de Atabapo and the mouth of Río Meta into the Río Orinoco. The original collector, Hans Willi Schwartz, told us that *P. simulans* also occurs in the upper Rio Negro areas between the mouth of the Rio Branco and the Río Orinoco headwaters and that although the ranges of *P. axelrodi* and *P. simulans* occur in the same general geographical areas, they in fact do not live in the same portions of the tributaries of large rivers such as the Rio Negro and Río Orinoco. He found *P. simulans* in the upper sections of these tributaries away from the main river and *P. axelrodi* in the lower portions, in the *varzea* and *terra firme* areas. Both species live in *terra firme* streams but apparently not in the same localities.

Description. See Table 1 for morphometrics and meristics of individual population samples. Morphometrics given below are totals for all samples, including some not recorded in Table 1. Specimens from Venezuela were not measured and scales could not be counted because they were partly deossified and very soft, having been in unbuffered formalin for several years. Specimens measured from vicinity of Puerto Correño are aquarium imports, most of which were preserved a few weeks after reaching the United States. We offer these measurements only as the best available for this species and point out that aquarium and transportation conditions may have altered the growth of these specimens.

Body moderately elongate, not compressed, greatest depth at a vertical line near origin of pelvic fins. Predorsal body profile moderately convex to nape where it is concave. Dorsal profile of head slightly convex. Body profile very slightly or not at all elevated at dorsal-fin origin; slightly convex or straight along dorsal-fin base; straight to slightly convex between dorsal-fin base and adipose-fin origin.

TABLE 1. MORPHOMETRICS AND MERISTICS OF *Paracheirodon simulans*.†

		Colombia, Puerto Correño				
			Range			
	Paratype	n	Low	High	$\bar{X}$	SD
Standard length	15.4	25	9.6	20.2	15.7	
Greatest body depth	29.9	25	25.0	31.3	28.1	1.525
Snout to dorsal-fin origin	56.5	24	51.2	55.2	53.5	1.226
Snout to pectoral-fin origin	27.9	25	23.8	30.2	27.2	1.395
Snout to pelvic-fin origin	51.3	24	46.8	51.8	49.5	1.105
Snout to anal-fin origin	65.6	25	58.6	66.3	63.3	1.792
Eye to dorsal-fin origin	41.6	24	35.7	42.1	38.2	1.482
Dorsal-fin origin to caudal-fin base	49.4	24	45.5	52.1	49.9	1.561
Caudal peduncle depth	11.7	25	8.3	11.0	10.1	0.699
Caudal peduncle length	15.6	25	14.2	17.9	16.2	0.757
Pectoral-fin length	16.9	25	16.0	19.8	18.2	1.020
Pelvic-fin length	12.3	23	12.7	16.3	14.7	0.890
Dorsal-fin base length	12.3	24	10.2	12.9	11.4	0.676
Longest dorsal-fin ray length	25.3	22	21.9	26.9	24.2	1.293
Anal-fin base length	23.4	25	22.0	26.3	23.6	1.108
Longest anal-fin ray length	18.8	22	16.7	21.7	19.6	1.279
Bony head length	26.0	25	21.9	28.1	24.9	1.248
Horizontal eye diameter	42.5	25	39.6	51.4	44.2	3.068
Snout length	22.5	25	16.1	23.8	19.7	1.914
Least bony interorbital width	32.5	23	29.6	36.4	32.6	1.972
Upper jaw length	35.0	25	32.4	43.8	35.9	2.741
Branched dorsal-fin rays	8	31	7	8	7.7	0.445
Branched pectoral-fin rays	8	32	7	9	8.1	0.354
Branched pelvic-fin rays	6	32	5	6	6.0	0.177
Branched anal-fin rays	15	32	14	18	16.0	0.822
Horizontal scale rows between dorsal fin and pelvic fin	9	22	9	9	9.0	0.000
Predorsal scales	10	22	10	10	10.0	0.000
Perforated lateral-line scales	—	20	0	5	2.6	1.569
Lateral series scales	32	21	29	32	30.9	0.700
Horizontal scale rows around caudal peduncle	12	22	12	12	12	0.000
Dorsal-limb gill rakers	6	42	5	6	5.9	0.328
Ventral-limb gill rakers	11	42	10	12	11.2	0.484
Vertebrae	32	42	32	33	32.4	0.507

† Paratype USNM 197510 and from Puerto Correño, Colombia, USNM 216737, USNM 216736, USNM 21091, and MCZ 52339. Standard length is expressed in mm. The next 16 measurements (through head length) are percentages of standard length. The following four measurements are percentages of bony head length.

Caudal peduncle slightly concave in both dorsal and ventral profiles. Dorsal fin midway between caudal-fin base and snout tip or slightly nearer caudal-fin base. Ventral body profile slightly convex from anterior tip of lower jaw to posterior anal-fin termination.

Head and snout relatively short, snout blunt. Mouth terminal. Gape angled somewhat anterodorsally from mandibular joint to snout tip. When mouth closed, maxilla extends posteriorly to a point approximately on a vertical line drawn ventrally from anterior border of pupil.

Dorsal-fin rays ii-7 to ii-8, usually ii-8 (rarely iii-8 with first unbranched ray extremely short), n = 34; adipose fin present in all specimens; anal-fin rays iii-15 to iii-

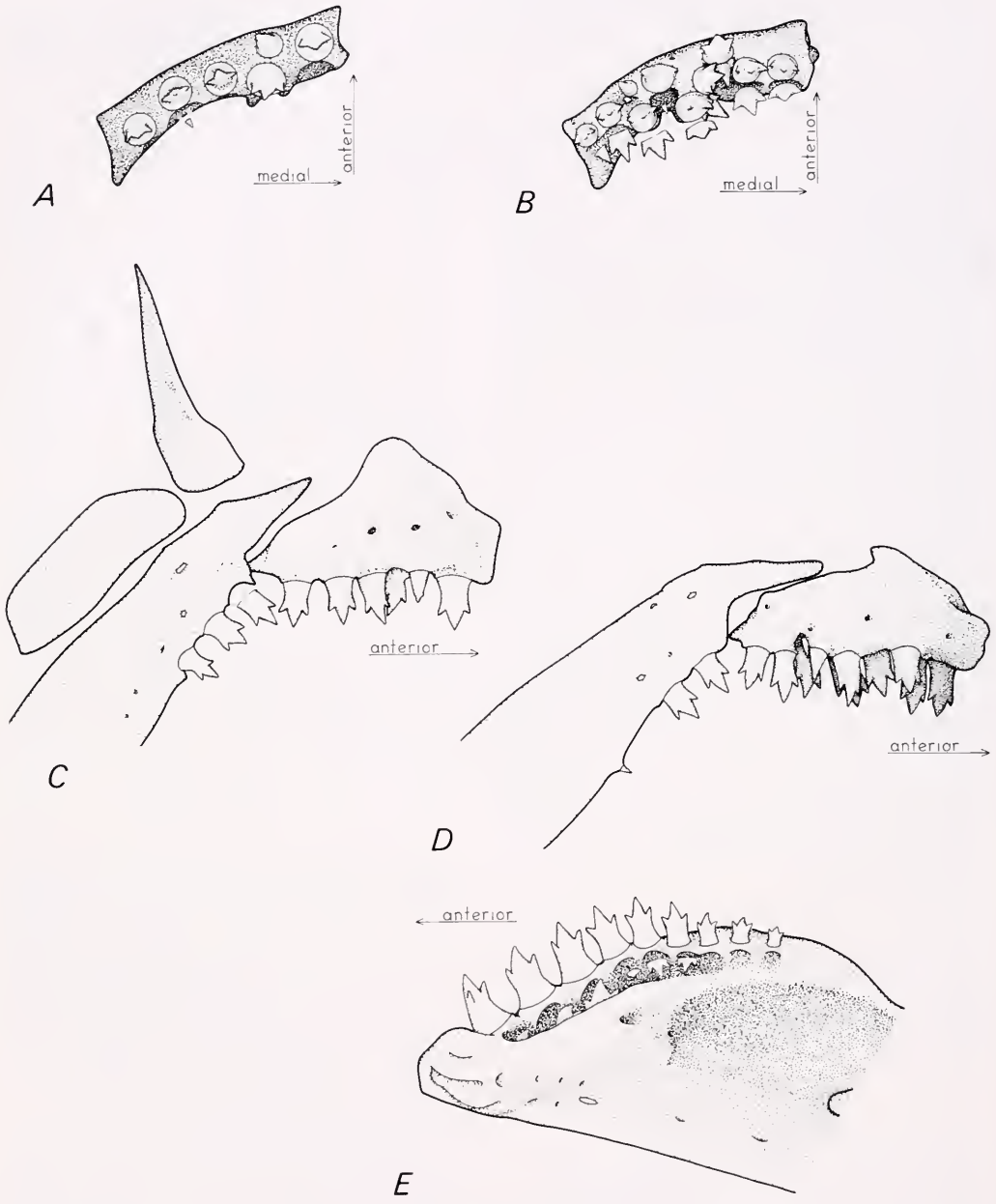

Figure 23. Teeth and jaws of *Paracheirodon innesi*. A. Premaxilla, ventral view of 4 year adult, SL 25.7 mm, USNM 216912. B. Premaxilla, ventral view of 4 year adult, SL 24.6 mm, USNM 216912. C. Premaxilla, maxilla, infraorbital 1, and antorbital (nasal is absent), anterolateral view, right side of adult, SL 25.7 mm, USNM 216912. D. Premaxilla and maxilla, anterolateral view, right side of adult, SL 24.6 mm, USNM 216912. E. Dentary, medial view, right side of adult, SL 25.4 mm, USNM 216912.

18, usually iii-16 (once iv-16 and twice iv-17), n = 34; pectoral-fin rays i-7 to i-9, usually i-8, n = 34; pelvic-fin rays i-5 to i-6, (only one specimen with i-5), n = 34; caudal-fin rays 10/9, n = 34. No bony pelvic-fin hooks found in mature male specimens.

Scales cycloid. Lateral line incomplete (or absent, one specimen), perforated lateral-line scales 0 to 5, usually 3, n = 24; scales in a lateral series 29 to 33, usually 31, n = 25; scale rows between anterior dorsal-fin base and pelvic-fin base 9, n = 28; predorsal scales 9 to 10, usually 10 (9 in one specimen), n = 28; horizontal scales rows around caudal peduncle 12, n = 28.

Dorsal-limb gill rakers 5 to 7, usually 6, n = 42; ventral-limb gill rakers 10 to 12, usually 11, n = 42.

Total number of vertebrae including Weberian apparatus and terminal compound centrum 32 to 34, usually 32, n = 32.

Dental Morphology. Premaxilla with two tooth rows, an inner row of four to five multicuspid teeth and an outer row of one to two conical teeth (Fig. 19A–E). Smallest specimens available to us, SL 11.1 and 11.4 mm, all USNM 216911, with four inner row premaxillary teeth; available specimens larger than preceding all with five. Tooth-cusp formula variable in the wild-caught specimens; representative cusp numbers 6653 [6 (median tooth), 6 (tooth lateral to median tooth), 5 (next lateral in series), 3 (lateral tooth)] (in a specimen 11.4 mm SL), 67763 (SL 11.8 mm), and 69865 (SL 13.8 mm), USNM 216911. Note that in larger specimens two teeth immediately lateral to symphyseal tooth have greatest number of cusps. Positive correlation occurs between fish size and total number of cusps on inner-row teeth, based on our small sample of wild-caught specimens (USNM 216911), SL 11.1 to 13.8 mm, n = 7, $\bar{X}$ = 12.2. In these specimens, total cusp number (added over all inner row teeth) gave regression statistics of: y-intercept = 26.0; slope = 4.3; correlation coefficient = 0.87. The few adult specimens available are aquarium raised and are not analyzed statistically; nevertheless, we report SL and tooth formula here for comparison with wild-caught juveniles: SL 20.2 mm, 79977; SL 21.1 mm, 57655; SL 23.9 mm, 68755; all USNM 216736. The degree of variability of these three specimens may be the result of their artificial diet. Nevertheless, the "adult" tooth configuration may be reached at about SL 13 to 14 mm. A more precise statement is not possible since we have no wild-caught adults. We cannot describe the "adult" configuration with certainty but only estimate it from the samples at hand.

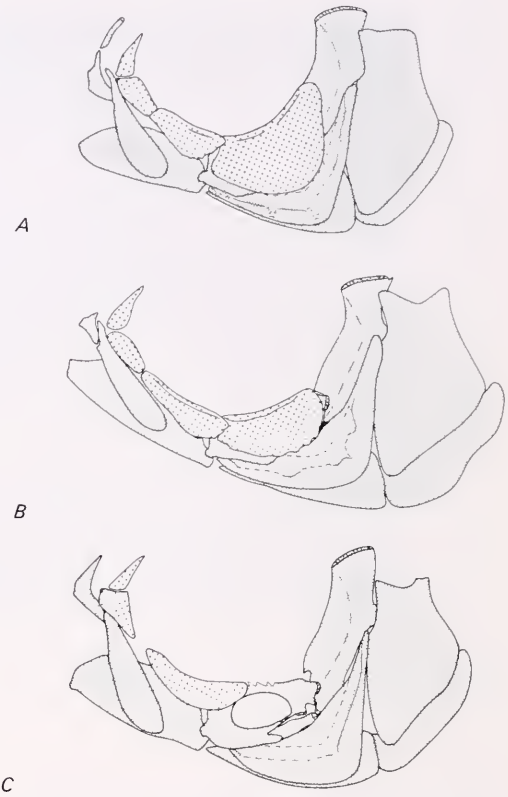

Figure 24. Face bones of the neon tetras. Circumorbital bones represented by plus-sign (+) pattern. Lateral view, left side. A. *Paracheirodon axelrodi*, SL 31.3 mm, USNM 216910. B. *Paracheirodon innesi*, SL 16.4 mm, MCZ 52156. C. *Paracheirodon simulans*, SL 20.4 mm, USNM 216738.

Figure 25. *Paracheirodon simulans*, collected from near Puerto Correño, Colombia, either in Venezuela or Colombia, USNM 216973, female above, SL 20.1 mm, male below, SL 17.6 mm.

There is usually a single, conical, outer row premaxillary tooth but occasionally a second tooth also is present. Again, our limited sample prevents a definitive statement about tooth numbers, but the number of outer row teeth apparently is not correlated with body size longer than about 11 mm SL since two teeth are present in specimens SL 11.5 and 13.5 mm (USNM 216911) and a single tooth is present in other wild-caught specimens. Tooth replacement patterns confirm that the outer tooth row in *P. simulans* is a "true" second row. In Figure 19A replacement trenches (see Roberts, 1967) are clearly visible posterior to the two outer row teeth and small replacement teeth are present in the trenches. Figure 19E is a diagrammatic representation from the anterior aspect of the same premaxilla illustrated in Figure 19A; in it the conical outer row replacement teeth are visible dorsal to the functional conical teeth. Note in both figures that the developing multicuspid replacement teeth (embedded in fleshy tissue) for the inner tooth row lie posterodorsal to the functional teeth. Maxillary teeth are not present in examined specimens, with the exception of one conical tooth on one side of a single specimen (14.4 mm SL) from USNM 216915.

A single row of six to nine teeth is present on the dentary, the medial four teeth being larger (Fig. 19F). Specimens from USNM 216911, discussed above, have the following tooth formula (from the symphysis laterally): (tooth 1) seven to nine, usually seven cusps; (tooth 2) six to seven, usually seven cusps; (tooth 3) five to seven cusps, usually seven cusps; (tooth 4) three to seven, usually three or five cusps; (tooth 5) one to three, usually one cusp; remainder conical. In our small sample of juvenile fish we found no apparent correlation between the cusp number and the SL.

Color Pattern. In life, *P. simulans* (Fig.

1) back olive brown with reticulate dark chromatophore pattern as described for color in alcohol, below. Intense iridescent blue-green lateral stripe extends from skin over infraorbital bones, over cornea of eye (evenly distributed over cornea), over cheeks and opercle, along sides of body, and ends at caudal-fin base. Blue lateral stripe broadest at vertical from pelvic-fin insertion or from just anterior to pelvic-fin insertion. Dense stripe of black chromatophores visible dorsal to blue-green stripe, broadest in region between opercle and posterior termination of dorsal-fin base. Poorly defined stripe of scattered dark chromatophores present ventral to blue lateral stripe. Numerous erythrophores scattered along myosepta between lateral blue stripe and anal-fin base, and scattered anteriorly as far as a point midway between opercle and pelvic-fin base in some specimens. In most specimens, erythrophores extend only slightly anterior to a vertical from pelvic-fin insertion. When erythrophores expanded, entire area between lateral blue stripe and anal-fin base red; when erythrophores contracted, area between blue stripe and anal-fin base light reddish brown. Belly silvery white, reflecting light blue ventrally under some light conditions. Fins hyaline except for very pale white area in some specimens along anterior three fin rays of dorsal fin; in anterior region of anal fin, extending to posterior border of anterior branched fin ray; and in center of adipose fin.

Compared to *P. innesi* and *P. axelrodi*, *P. simulans* with more green in lateral stripe and red sides less brilliant (sometimes virtually lacking in disturbed individuals). Iridescent green covers more of head, i.e., more of eye, infraorbitals, cheeks, and opercle. Blue-green lateral stripe broader in proportion to that of those species.

In alcohol, *P. simulans* (Fig. 25) with ground color light cream brown. Scale pocket margins of dorsum and two to three ventrally successive lateral scale rows lined with dark brown chromatophores, giving a reticulate pattern. Small brown chromatophores may be scattered within scale pocket areas defined by marginal dark chromatophores. Midlateral stripe extends from just posterior to eye to dorsal half of caudal-fin base. Large dark chromatophores on infraorbital 1 probably an anterior extension of lateral stripe. Dorsal border of lateral stripe lies about two and a half scale rows ventral to dorsal-fin origin; maximum width of lateral stripe about three scales. Belly sometimes with a few scattered dark chromatophores. Peritoneum with numerous dark chromatophores, more obvious in smaller specimens. Numerous small dark chromatophores over tips of jaws and dorsum of head, these extending as thin line to caudal-fin base, marking dorsal midline. Dark chromatophores sparsely distributed over infraorbitals and opercle. Numerous small dark chromatophores present along ventral border of orbit. Small dark chromatophores lie along anal-fin base and along line marking conjunction of anal-fin musculature and hypaxial body musculature; these lines converge at posterior termination of anal-fin base and continue as a well-defined dark line along ventral edge of caudal peduncle. Small dark chromatophores line fin-ray borders of all fins; interradial membranes without dark chromatophores. Adipose fin without chromatophores or with very few small dark chromatophores.

Paracheirodon axelrodi (Schultz)
Figures 2, 4, 5, 7, 20, 24A, 26; Tables 2, 4 to 7

Cheirodon axelrodi Schultz, 1956: 42, original description, Brazil "somewhere near Porto Velho, Amazonas" (see discussion, Appendix 2).—Axelrod, 1956: 16, type locality.—International Commission of Zoological Nomenclature 1957: 87, priority of *Cheirodon axelrodi* in favor of *Hyphessobrycon cardinalis*.—Géry, 1960b: 8, relationships.—Géry, 1963: 71, relationships.—Post, 1965: 47, chromosome numbers.—Scheel and Christensen, 1970: 24, relationships based on chromosomes.—Scheel, 1972: 60, relationships based on

chromosomes.—Géry, 1977: 546, 563, relationships.—Kullander, 1978: 274, comments on distribution.

Hyphessobrycon cardinalis Myers and Weitzman, 1956: 1, original description, Brazil, "Rio Negro, Amazonas" (see discussion, Appendix 2).—Meinken, 1956: 89, type locality.—Ladiges, 1956: 116, discovery.—Hoedeman, 1956: 154, type locality, name priority and relationships.—Weitzman, 1956: 257, type locality.

Specimens Examined. Holotype, USNM 164483, SL 22.4 mm; 1, paratype, USNM 164484, SL 20.0 mm, Brazil, Amazonas, stream near Tomar (=Thomar) (0°25'S, 63°55'W), Rio Negro, 1956, collected for Paramount Aquarium Inc. [Note: original locality listed by Schultz (1956) as "near Porto Velho, Brazil," (State of Rondonia, Brazil) discussed in Appendix 2.] Holotype, *Hyphessobrycon cardinalis* (=*P. axelrodi*), CAS(SU) 48710, SL 22.5 mm, 8 paratypes, CAS(SU) 48711, and 2 alizarin preparations CAS(SU) 48712, SL 19.5–21.5 mm, Brazil, Amazonas, Rio Negro near Tomar (0°25'S, 63°55'W), "winter of 1955–1956," for Paramount Aquarium Inc. [Note: original type locality given as "Rio Negro, Amazonas, Brazil;" more precise locality data above originally withheld from publication at request of Paramount Aquarium Inc.].—10, USNM 216901, SL 10.5–24.5 mm, Brazil, Amazonas, Rio Negro, an igarapé of varzea at Tapurucuara (1°30'N, 65°2'W), 19 October 1972, Paulo Vanzolini for EPA.—Following lots with same locality data as USNM 216901 immediately preceding: 15, MZUSP; 5, ANSP 138018, SL 12.3–24.1 mm.—6, USNM 216900, SL 14.7–24.4 mm, Brazil, Amazonas, Rio Negro, São João near Tapurucuara (1°30'N, 65°2'W), 24 October 1972, Paulo Vanzolini for EPA.—Following lots with same locality data as USNM 216900 preceding: 6, MCZ 52460, SL 11.4–22.3 mm; 13, MZUSP; 5, MZUSP; 5, USNM 216905, SL 22.5–25.0 mm; 30, MZUSP; 10, USNM 216902, SL 12.0–22.8 mm; 8, MCZ 52461, SL 11.5–20.0 mm; 17, MZUSP; 7, USNM 216899, SL 12.2–20.5 mm; 7, CAS 39167, SL 11.8–20.5 mm; 8, MZUSP; 7, USNM 216908, SL 12.3–24.4 mm; 24, MZUSP; 9, USNM 216898, SL 10.4–22.6 mm; 6, BMNH 1977.4.20.11–16, SL 11.2–24.0 mm; 5, ZMA 115.065, SL 13.7–21.0 mm.—7, USNM 216907, SL 12.5–24.5 mm, Brazil, Amazonas, Rio Negro, São João near Tapurucuara (1°30'N, 65°2'W), 27 October 1972, Paulo Vanzolini for EPA.—With same data as USNM 216907 immediately preceding: 6, MZUSP; 6, USNM 216909, SL 13.1–24.5 mm.—17 alizarin preparations, USNM 216740, SL 13.6–24.2 and 10, USNM 216739, SL 20.2–24.8 mm, Brazil, Amazonas, "tributaries of upper Rio Negro," September–October 1975, from Cardinal Aquarium, Manaus, Brazil through Ross Socolof.—4, NRM THO/1977228.4088, SL 20.8–23.1 mm, Colombia, Guainia, Caño Bacon, pueblo Bretonia, about 3°39'N, 68°05'W, June 2–6, 1972, T. Hongslo.—11, NRM THO/197207.3049, SL 19.7–26.7, same locality data as preceding but collected May 27, 1972 by Hongslo.—7, NRM THO/1972230.3035, SL 14.5–16.7, Colombia, Guainia, Caño Bacon, Puerto Nariño, about 3°36'N, 68°15'W, June 6, 1972, T. Hongslo.—1, NRM THO/1972106.3133, SL 13.8 mm, Colombia, Vichada, Río Guarrojo, near its mouth, about 4°07'N, 70°45'W, March 11, 1972, T. Hongslo.—1, NRM THO/1972103.4155, SL 13.4 mm, same locality data as preceding but collected March 8, 1972.—2, NRM THO/1972103.3060, SL 11.8–12.5 mm, same data as preceding.—34, USNM 216903, SL 10.1–23.7 mm and 4 alizarin preparations, USNM 216916, SL 10.1–15.2 mm, Colombia, Vichada, Caño Muco (4°16'N, 70°20'W), 2 April 1974, J. E. Thomerson and party.—Following lots with same locality data as USNM 216903 immediately preceding: 15 alizarin preparations, MCZ 52459, SL 10.1–13.9 mm; 10, ANSP 138017, SL 10.9–13.2 mm; 10, BMNH 1977.4.20.1–10, SL 11.5–13.0 mm; 10, CAS 39147, SL 10.8–12.0 mm.—7, USNM 231737, SL 11.3–23.4 mm, Colombia, Vaupés, Río Vaupés at Mitú (1°7'N, 70°4'W), November 1964, H. R. Axelrod.—5, USNM 216756, SL 12.1–13.6 mm and 5, MBUCV-V 6095, Venezuela, Amazonas, small caño tributary to Rio Casiquiare near Beripomoni (2°4'N, 66°9'W), 28 January 1969, Antonio Machado and Jose Mosco.—6, USNM 216759, SL 22.2–27.5 mm, Venezuela, Amazonas, Caño Morocoto, Río Orinoco drainage, vicinity of San Fernando de Atabapo (4°4'N, 67°42'W), 13 February 1974, A. Cortez.—Following lots with same locality data as USNM 216759 immediately preceding: 6, MBUCV-V 9640, SL 23.4–27.1 mm; 4, ANSP 137965, SL 23.0–26.6 mm; 4, BMNH 1977.3.11.1–4, SL 22.2–28.3 mm; 5, MCZ 52341, SL 23.2–28.8 mm; 7, USNM 216760, SL 13.2–19.1 mm; 9, ANSP 137963, SL 13.2–16.5 mm; 9, MCZ 52340, SL 13.0–16.8 mm.—3, USNM 216897, SL 13.5–14.7 mm, Venezuela, Amazonas, caño near Sipapo (2°6'N, 66°28'W), left bank of Rio Casiquiare, 1 February 1969, Antonio Machado and Jose Mosco.—Following lots with same locality data as USNM 216897 immediately preceding: 3, MBUCV-V 6980, SL 13.4–16.5 mm; 3, ANSP 138019, SL 13.8–15.8 mm; 4 alizarin preparations, USNM 216914, SL 14.4–15.4 mm.—10, USNM 216754, SL 10.3–12.0 mm and 10, MBUCV-V 8017, Venezuela, Amazonas, Caño Caranaven, tributary to Rio Orinoco near San Fernando de Atabapo (4°4'N, 67°42'W), 4 December 1973, A. Cortez and R. Navarro.—2, USNM 216755, SL 13.9–14.3 mm, Venezuela, Amazonas, Caño Pamoni (2°50'N, 65°54'W), 28 Janaury 1969, Francisco Mago-Leccia, Antonio Machado, Jose Mosco.—121, USNM 236841, SL 11.0–25.9 mm, Brazil, Amazonas, tributary to Igarapé Tarumã Açu, about 20 km north of Manaus on road between Manaus and Itacoatiara (Serpa) (2°55'S, 60°00'W), 18 November 1979, Michael Goulding, Marilyn Weitzman, Stanley H. Weitzman (this locality is an introduction).—21 alizarin preparations, USNM 216910, SL 12.8–33.1 mm, locality unknown, aquarium specimens.—11, USNM 216904, SL 21.9–31.4 mm, locality unknown, aquarium specimens.

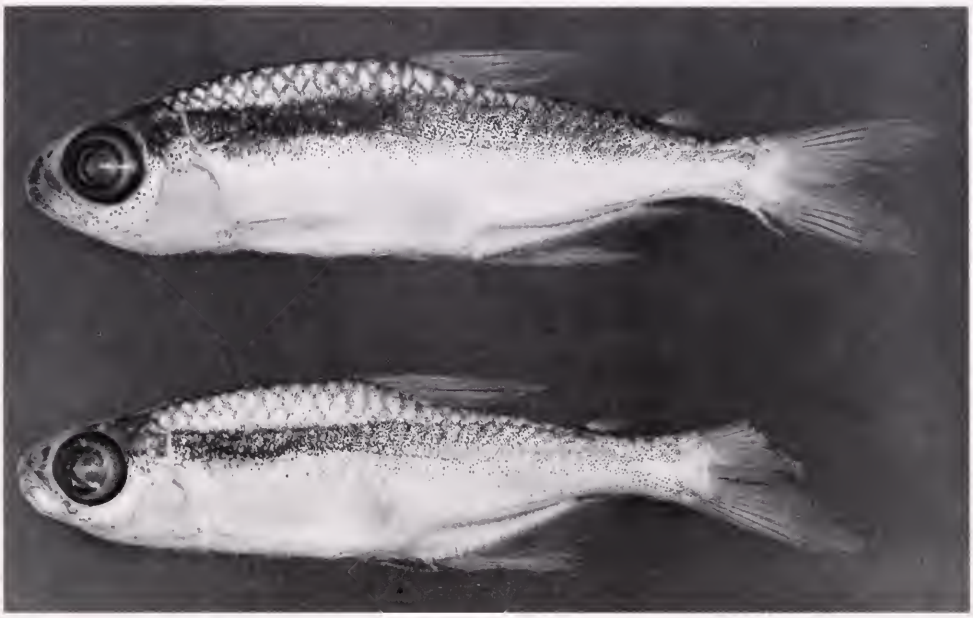

Figure 26. *Paracheirodon axelrodi*, Brazil, Amazonas, Rio Negro at São João near Tapurucuara, USNM 216905, female above, SL 24.6 mm, male below, SL 22.5 mm.

Paracheirodon axelrodi occurs in the upper Rio Negro region from the region of Tapurucuara west to at least the lower regions of the Río Vaupés in Colombia (=Rio Uaupes in Brazil), the Río Içana, the Río Guainia northward up the Rio Casiquiare in Venezuela and the headwater area of the Río Orinoco. It very probably occurs in the adjacent regions of the Río Sipapo and the Río Atabapo of Venezuela, and the Río Inirida, Río Guaviare, Río Vichada, and Río Meta of Colombia. This species has escaped and is reproducing in at least one stream, a tributary of the Igarapé Tarumã Açu, about 20 km north of Manaus. See Appendix 2 for discussion of the type locality.

Description. See Table 2 for morphometrics and meristics of individual population samples. Morphometrics given below are total ranges for all samples including some not in Table 2. Aquarium specimens are excluded.

Body moderately elongate, not compressed. Greatest body depth at or slightly anterior to dorsal-fin origin. Predorsal body profile moderately convex to area dorsal to eye. Body profile concave at nape. Body profile somewhat elevated at dorsal-fin origin; slightly convex or nearly straight along dorsal-fin base; slightly convex between dorsal-fin base and adipose-fin origin. Caudal peduncle concave in both dorsal and ventral profiles. Dorsal fin midway between caudal-fin base and snout tip or slightly nearer snout tip. Ventral body profile slightly convex from anterior tip of lower jaw to posterior anal-fin termination. In specimens which appear starved, Figure 29, belly profile may be nearly straight.

Head and snout relatively short, snout blunt. Mouth nearly terminal with lower jaw slightly included when mouth fully closed. Gape angled somewhat anterodorsally from mandibular joint to snout tip. When mouth closed, maxilla extends posteriorly to a point approximately on a vertical line drawn ventrally from anterior border of pupil.

Dorsal-fin rays ii-8 to ii-9, usually ii-9, n = 91; adipose fin present; anal-fin rays

TABLE 2. MORPHOMETRICS AND MERISTICS OF *Paracheirodon axelrodi*.†

		Venezuela, Morocoto					Colombia, Caño Muco					Brazil, Tapurucuara					Total R	
			Range					Range					Range					
	Holotype	*n	Low	High	$\bar{X}$	SD	n	Low	High	$\bar{X}$	SD	n	Low	High	$\bar{X}$	SD	Low	
Standard length	22.0	7	11.6	18.5	14.4		18	11.0	23.4	13.3		59	10.5	25.1	17.7		10.5	25.1
Greatest body depth	31.8	7	23.7	27.6	25.8	1.513	18	26.4	30.1	28.3	1.028	59	24.0	30.7	27.3	1.644	23.7	30.9
Snout to dorsal-fin origin	52.7	7	50.7	54.3	52.5	1.252	18	52.1	54.9	53.3	0.814	59	50.3	56.0	52.7	1.049	50.3	56.0
Snout to pectoral-fin origin	26.4	7	27.6	31.9	30.1	1.606	18	26.9	32.0	30.7	1.344	59	26.8	34.4	30.3	1.818	26.4	34.4
Snout to pelvic-fin origin	50.5	7	48.6	50.7	49.4	0.780	18	49.2	54.3	50.6	1.159	59	46.3	52.6	49.0	1.204	46.3	54.3
Snout to anal-fin origin	66.4	7	61.8	65.9	64.4	1.389	18	61.2	65.4	63.8	0.965	59	59.8	67.2	63.6	1.313	59.8	67.2
Eye to dorsal-fin origin	36.8	7	34.3	36.0	35.3	0.581	18	34.8	37.3	35.9	0.790	59	33.5	39.8	35.8	1.354	33.5	39.8
Dorsal-fin origin to caudal-fin base	55.5	7	49.1	52.5	50.6	1.125	18	50.0	54.6	51.8	1.237	59	49.0	55.2	52.0	1.240	49.0	55.5
Caudal-peduncle depth	10.5	7	8.0	12.0	9.6	1.353	18	9.4	10.9	10.1	0.358	59	8.3	10.3	9.3	0.502	8.0	12.0
Caudal-peduncle length	14.5	7	15.3	16.8	16.0	0.512	18	14.4	16.7	15.6	0.597	59	14.8	18.6	16.5	0.750	14.5	18.6
Pectoral-fin length	—	4	17.6	19.8	19.0	1.017	16	15.7	19.7	17.9	1.146	54	16.2	23.8	19.3	1.497	15.7	23.8
Pelvic-fin length	15.5	7	13.5	16.8	14.9	1.538	18	14.1	17.5	16.1	0.733	58	13.4	21.8	17.3	1.630	13.4	21.8
Dorsal-fin base length	14.4	7	12.7	13.9	13.5	0.443	18	12.7	14.8	14.0	0.572	59	12.0	15.2	13.6	0.660	12.0	15.2
Longest dorsal-fin ray length	27.3	6	27.2	28.4	28.0	0.450	15	26.8	30.4	28.5	1.031	55	25.7	33.0	28.6	1.508	25.7	33.0
Anal-fin base length	23.2	7	22.4	23.7	23.0	0.486	18	22.1	25.5	23.7	0.887	59	21.7	26.0	23.9	0.963	21.7	26.0
Longest anal-fin ray length	20.5	2	23.2	23.9	23.6	0.495	14	22.6	25.8	24.1	1.000	56	21.9	26.3	23.9	1.022	20.5	26.3
Bony head length	25.9	7	26.5	30.2	28.3	1.421	18	25.2	30.2	28.9	1.086	59	24.7	32.2	28.2	1.714	24.7	32.4
Horizontal eye diameter	40.4	7	40.8	45.7	43.4	1.506	18	40.7	48.6	44.2	1.682	59	39.1	45.9	42.2	1.508	39.1	45.9
Snout length	19.3	7	16.7	19.4	18.0	0.911	17	13.9	20.3	17.2	1.507	59	16.2	23.0	19.4	1.570	13.9	23.0
Least bony inter-orbital width	28.1	7	25.0	27.0	26.0	0.675	17	25.0	29.7	27.2	1.472	58	22.0	30.4	26.2	1.898	22.0	30.4
Upper jaw length	35.1	7	30.6	33.3	31.3	0.945	16	28.2	32.4	30.5	1.267	58	24.5	39.5	32.0	2.573	24.5	39.5
Branched dorsal-fin rays	9	13	8	9	8.8	0.376	18	9	9	9	0.000	48	8	9	8.9	0.309	8	9
Branched pectoral-fin rays	11	13	10	11	10.2	0.439	18	10	11	10.8	0.428	48	10	11	10.6	0.483	10	11
Branched pelvic-fin rays	7	13	7	7	7	0.000	18	7	7	7	0.000	48	7	7	7	0.000	7	7
Branched anal-fin rays	17	13	14	17	16.0	0.707	18	15	17	16.2	0.618	48	15	19	16.6	0.841	14	19

TABLE 2. CONTINUED.

		Venezuela, Morocoto					Colombia, Caño Muco					Brazil, Tapurucuara					Total R	
			Range					Range					Range					
	Holotype	*n	Low	High	X̄	SD	n	Low	High	X̄	SD	n	Low	High	X̄	SD	Low	
Horizontal scale rows between dorsal fin and pelvic fin	9	8	9	9	9	0.000	3	9	9	9	0.000	43	9	9	9	0.000	9	9
Predorsal scales	—	13	9	10	9.4	0.506	4	9	9	9	0.000	26	9	11	9.9	0.628	9	11
Perforated lateral-line scales	7	7	5	7	6.0	0.577	1	6	6	—	—	26	5	8	6.5	0.762	5	8
Lateral series scales	31	7	30	33	31.0	1.000	1	31	31	—	—	22	30	32	31.3	0.767	30	33
Horizontal scale rows around caudal peduncle	12	8	12	12	12	0.000	1	12	12	—	—	26	12	12	12	0.000	12	12
Dorsal-limb gill rakers	7	13	6	8	6.9	0.641	18	6	7	6.7	0.461	35	6	8	7.1	0.404	6	8
Ventral-limb gill rakers	12	13	12	14	12.8	0.555	18	12	14	12.6	0.608	36	11	13	12.3	0.535	11	14
Vertebrae	32	12	31	33	32.0	0.426	18	31	33	32.1	0.416	64	31	33	32.2	0.420	31	33

† Holotype USNM 104483; Rio Morocoto, Venezuela, USNM 216760, USNM 216759; Caño Muco, Colombia, USNM 216903; Tapurucuara, Brazil, USNM 216901, USNM 216900, USNM 216905, USNM 216902, USNM 216899, USNM 216898, USNM 216908, USNM 216907, USNM 216909, USNM 216740, ANSP 138018, MCZ 52460, MCZ 52461, CAS 39167, ZMA 115.065, BMNH 1977.4.20.11–16. Standard length is expressed in mm. The next 16 measurements (through head length) are percentages of standard length. The next four measurements are percentages of bony head length.

* Six specimens were raised to adult size in an aquarium and were not included in the measurements.

iii-14 to iii-19, usually iii-16 or iii-17, n = 91; pectoral-fin rays i-10 to i-11, usually i-11, n = 91; pelvic-fin rays i-7, n = 91; and caudal-fin rays 10/9, n = 91. Bony pelvic-fin hooks present in mature male specimens equal to or longer than 17.3 mm SL; some immature males between 17.0 and 19.5 mm SL without hooks, all males longer than 19.5 mm SL mature and with pelvic-fin hooks.

Scales cycloid. Lateral line incomplete; perforated lateral-line scales 5 to 8, usually 6 or 7, n = 35; scales in a lateral series 30 to 33, usually 31, n = 31; scale rows between anterior dorsal-fin base and pelvic-fin base 9, n = 55; predorsal scales 9 to 11, usually 10, n = 41; horizontal scale rows around caudal peduncle 12, n = 36.

Dorsal-limb gill rakers 6 to 8, usually 7, n = 67; ventral-limb gill rakers 11 to 14, usually 12 or 13, n = 67.

Total number of vertebrae including Weberian apparatus and terminal compound centrum 31 to 33, usually 32, n = 77.

Dental Morphology. A single row of five premaxillary teeth, each with five cusps, is present in adults (Fig. 20A,B). Specimens of about 10 mm SL have five to six tricuspid teeth (Fig. 20C). During ontogeny replacement teeth usually have four or five cusps (Fig. 20D), with the adult configuration of cusps reached at about 18 mm SL. Specimens smaller than this size have five to six premaxillary teeth; specimens larger consistently have five teeth. Cusp number is not increased with increased SL in available specimens caught in the wild. A single maxillary tooth with five cusps usually is present in adult *P. axelrodi* (Fig. 20B). Ontogenetic replacement of teeth with fewer cusps by teeth with more cusps occurs as with the premaxillary teeth (compare Fig. 20B,D). Juveniles of about 10 mm SL lack maxillary teeth (Fig. 20C). Our small sample of wild-caught juveniles shows teeth with one to three cusps in fishes 11 to 15 mm SL, four to five cusps in fishes 16 to 18 mm SL, and five cusps in specimens larger than 18 mm SL.

Dentary teeth lie in a single row, numbering 5 to 11, usually 7 or 8. The anteromedial three or four teeth are largest, with three to seven, usually five, cusps; laterally successive teeth are smaller, with concommitant decrease in cusp number (Fig. 20E,F). In specimens available to us, there is a slightly smaller total cusp number per dentary tooth in specimens less than about 14 mm SL than in larger specimens, indicating ontogenetic replacement by teeth with a greater number of cusps. We found no apparent correlation of dentary tooth number and SL.

Color Pattern. In life *P. axelrodi* (Fig. 2) back dark olive brown with reticulate dark chromatophore pattern, as described under color in alcohol, below. Intense iridescent blue to blue-green lateral stripe extends from skin over anterior infraorbital bones, over cornea of eye (usually concentrated dorsally), sparsely over cheeks, over opercle, and posteriorly to just ventral to posterior border of adipose fin. Blue lateral stripe broadest just anterior to a vertical from dorsal-fin origin. Dense stripe of black chromatophores visible dorsal to blue stripe, broadest in area between opercle and dorsal-fin origin. Broad stripe of loosely scattered dark chromatophores present ventral to blue lateral stripe, but usually not visible because of red pigment. Numerous erythrophores over sides of body ventral to blue stripe, extending ventrally approximately to a line between pectoral-fin origin and anus anteriorly and to anal-fin base and ventral border of caudal peduncle posteriorly. Numerous erythrophores also present anteriorly over ventral portion of opercle and posteriorly over dorsum of caudal peduncle, scales at caudal-fin base, and dorsally to ventral border of blue lateral stripe. In disturbed individuals with erythrophores contracted, very narrow stripe of pale brown present between blue lateral stripe and red area. Erythrophores immediately

dorsal to anal-fin base slightly less dense than in rest of red stripe; this area defined dorsally by narrow stripe of dark chromatophores extending to ventral border of caudal-fin base. Belly silvery white ventral to erythrophore area, reflecting blue under some light conditions. Fins hyaline except for faint white area along anterior anal-fin rays; indistinct whitish area along anterior border of dorsal fin and white area on adipose fin in some specimens.

Compared to *P. simulans*, *P. axelrodi* has a bluer stripe which posteriorly terminates ventral to the adipose fin, less blue on eye, and more intense red pigmentation over a wider area of the body. See also the live color description of *P. simulans*.

Compared to *P. innesi*, *P. axelrodi* has a slightly wider and longer blue stripe, much more widely distributed red pigment, and less distinct white markings on the anal fin. See also the live color description of *P. innesi*.

In alcohol *P. axelrodi* (Fig. 26) with ground color light cream brown. Scale pocket margins of dorsum and two ventrally successive lateral scale rows lined with light brown chromatophores, giving a reticulate pattern. Small brown chromatophores may lie scattered within scale pocket areas defined by marginal chromatophores. Midlateral stripe consists of two kinds of chromatophores: dense dark-brown chromatophores extend from just posterior to eye (where they extend onto dorsum of head, see below) to just ventral to adipose fin, lying along myosepta in that area; lighter brown, less dense and less numerous chromatophores lie just ventral to darker ones, extending from just posterior to opercle to caudal-fin base and slightly onto upper and lower caudal-fin lobes. Dorsal border of lateral stripe lies about two to two and a half scale rows ventral to dorsal-fin origin; maximum width of lateral stripe about two to two and a half scales. Small brown chromatophores may occur sparingly over belly and flanks dorsal to anal fin. Small dark chromatophores lie along anal-fin base and along a line marking conjunction of anal-fin musculature and hypaxial body musculature. Dark brown chromatophores cover head dorsally, extending anteriorly over tips of upper and lower jaws and posteriorly onto dorsum of body to caudal-fin base as thin line marking dorsal midline. Large dark chromatophores in area of infraorbital probably represent anterior extension of lateral stripe. Dark chromatophores distributed sparingly over infraorbital and preopercular area. A few dark chromatophores form a very thin margin on ventral border of orbit. Small chromatophores line fin-ray borders of all fins; interradial membranes without chromatophores. Adipose fin with small dark chromatophores, concentrated about at center of fin.

Specimens from MCZ 52241 exhibit much the same pigment patterns as those in MCZ 52460, but two kinds of chromatophores are not evident in lateral dark stripe. Densely arranged dark chromatophores extend posteriorly only to anterior of adipose-fin base; less numerous, usually smaller chromatophores extend posteriorly to caudal-fin base (becoming larger and more numerous posteriorly). Dark chromatophores also form a line over anal-fin base to ventral portion of caudal-fin base. Small dark chromatophores occur sparingly over ventral border of caudal peduncle, but these not organized into a stripe.

Specimens from MCZ 52459 much less pigmented than those described above. In these, dark chromatophores restricted almost entirely to head (as described above), dense lateral stripe (only one kind of chromatophore evident) which extends only to vertical from anal-fin origin, a few scale margins of dorsum, and along fin-ray borders.

Population Variation. For the most part our sample sizes are small and not suitable for studies of intraspecific variation. How-

Figure 27. *Paracheirodon innesi,* Colombia, Amazonas, Rio Loreto Yacu, male, SL 22.2 mm, MCZ 52156.

ever, some variation appears evident in the numbers of fin rays, scales, and gill rakers. As an example, using a two-tailed test and square root transformations in computing value of t, we found significant differences ($P < 0.01$) in numbers of branched pectoral-fin rays, branched anal-fin rays, predorsal scale number, and ventral-limb gill raker counts in population samples from Tapurucuara, Rio Negro, Amazonas, Brazil (n = 48) and Morocoto, Río Orinoco, Amazonas, Venezuela (n = 13). A study of the significance of this sort of variation in *P. axelrodi* in relation to geographic distribution must await intensive collections of samples throughout its range.

Paracheirodon innesi (Myers)
Figures 3, 8, 21, 22, 23, 24B, 27; Tables 3 to 7

Hyphessobrycon innesi Myers, 1936: 97, original description, Peru, "near Iquitos" (see discussion, Appendix 2).—Innes, 1936: 135, introduction into aquarium trade and source of type specimens.—Stoye, 1936: 137, type locality based on interview with collector August Rabaut.—Myers and Weitzman, 1956: 2, relationships.—Hoedeman, 1956: 154, relationships.—Géry, 1960b: 9, relationships.—Lueken and Foerster, 1969: 174, chromosome study.

Paracheirodon innesi (Myers), Géry, 1960b: 12, relationships, referral to new genus.—Géry, 1963: 70, relationships.—Post, 1965: 65, chromosome numbers.—Scheel and Christensen, 1970: 24, relationships based on chromosomes.—Scheel, 1972: 60, relationships based on chromosomes.—Géry, 1977: 587, relationships.

Cheirodon innesi (Myers), Van Ramshorst, 1981: 142, aquarium description, referral of *P. innesi* to *Cheirodon*.

Specimens Examined. Holotype, USNM 102109, SL 22.2 mm; Colombia, Amazonas, somewhere up the Río Putumayo, March–April 1936, August Rabaut. [Note: original type locality listed by Myers (1936) as "near Iquitos" in Peru was later discussed by Stoye (1936) and noted to be Río Putumayo in Colombia].—29, USNM 216699, SL 13.1–18.5 mm, Colombia, Amazonas, Río Loreto Yacu, in small creeks about 1 km from mouth of Río Loreto Yacu where it empties into Río Marañon (3°30'S, 70°10'W), 3 December 1976, Alfonso Doaz.—71 (13 of these alizarin preparations), MCZ 52156, SL 13.4–22.2 mm, same locality data as USNM 216699.—1, MCZ 52165, SL 18.5 mm, Colombia, Amazonas, small tributary of Lago Yahuacaca (4°5'S, 69°58'W) on Río Marañon (=Río Amazonas), December 1976, W. L. Fink.—1, USNM 216865, SL 19.1 mm, Colombia, Amazonas, near Leticia (4°14'S, 69°55'W), 4 December 1974, Donald Kramer.—1, MZUSP 13256, SL 14.3 mm, Brazil, Amazonas, Lago Miuá (3°48'S, 62°12'W), connecting with Rio Solimões somewhat west of Codajás, 25 September 1968, EPA.—8, USNM 216710, SL 12.6–15.0 mm, Brazil, Amazonas, near Rio Tapauá where it enters Rio Purus (5°45'S, 64°20'W), November 1963, H. R. Axelrod, H. Schultz, F. Terofal.—16, USNM 216912, SL 12.9–26.5 mm, aquarium specimens, 1974 (alizarin preparations).—10, USNM 216906, SL 23.6–25.5 mm, aquarium specimens, 1975.—28, NRM THO/1971371.3220, SL 13.3–16.3 mm, Brazil, Amazonas, Rio Javari, Lago Guariba, Caño de Guariba, about 4°12'S, 70°17'W, September 13, 1971, T. Hongslo.

The confirmed range of this species is in two disjunct areas. One is the area around Leticia and Ta-

batinga, in the lower course of the Rio Putumayo, and in small streams entering the Rio Solimões a few km downstream from Leticia. The second area is about 870 straight-line km east of the first region, near Codajás, and at least 400 straight-line km up the Rio Purus, a large river emptying into the Rio Solimões about 75 km east of Codajás. We doubt that the actual distribution of *P. innesi* is disjunct and we presume that *P. innesi* may have a wide distribution in western Brazil in tributaries along the Rio Solimões, in southeastern Colombia and in eastern Peru along the lowland tributaries of the Río Napo and the Río Putumayo which, as the Rio Içá, enters the Rio Solimões in Brazil. Sven Kullander, personal communication, states that *P. innesi* is present in the area around Janaro Herrrera (4°55'S, 73°40'W) on the Río Ucayali of Peru. Harald Schultz (1962: 43) reported neon tetras "... from the Japura ... southward to the region of Iquitos." He stated that neon tetras are found in all flowing blackwater streams of this region. Geisler (1979: 24) reported neon tetras from the Río Curaray, a tributary of the Río Napo in Peru. These last two localities are not represented by specimens in museums. In areas where *P. innesi* occurs it is always in blackwater or clearwater streams and is never found in whitewater streams with their headwaters in the Andes. This species is often temporarily held in aquarium compounds in diverse areas of South America. Its successful introduction into some of these areas with the proper ecological conditions may be inevitable and should be carefully screened for future zoogeographic considerations. See Appendix 2 for discussion of the type locality.

Description. See Table 3 for morphometrics and meristics of holotype and one population sample. Morphometrics given below are total ranges for all samples examined except aquarium specimens.

Body moderately elongate, not compressed. Greatest body depth at or slightly anterior to dorsal-fin origin. Predorsal body profile moderately convex to area dorsal to eye, sometimes concave at the nape. Body profile slightly elevated at dorsal-fin origin; slightly convex along dorsal-fin base; slightly convex between dorsal-fin base and adipose-fin origin. Caudal peduncle profile somewhat concave in both dorsal and ventral profiles or ventral one nearly straight. Dorsal fin midway between caudal-fin base and snout tip or nearer snout tip than caudal-fin base. Ventral body profile convex from anterior tip of lower jaw to posterior anal-fin termination. Often nearly straight between posterior tip of lower jaw and anus in wild-caught specimens (Fig. 27).

Head and snout relatively short with a blunt, rounded snout. Mouth terminal. Gape angled somewhat anterodorsally from mandibular joint to snout tip. Maxilla extends posteriorly to a point approximately on a vertical line drawn ventrally from anterior border of pupil.

Dorsal-fin rays ii-8 to ii-9, usually ii-9, n = 22; adipose fin present; anal-fin rays iii-16 to iii- or iv-19, usually iii-16 or iii-17, n = 22; pectoral-fin rays i-11 to i-13, usually i-12, n = 22; pelvic-fin rays i-6 to i-7, usually i-7, n = 22; caudal-fin rays 10/9, n = 22. Bony pelvic-fin hooks absent in all specimens.

Scales cycloid. Lateral line incomplete; perforated lateral-line scales 3 to 6, usually 5, n = 22; scales in a lateral series 30 to 33, usually 31, n = 21; scale rows between anterior dorsal-fin base and anterior pelvic-fin base 9, n = 21; predorsal scales 9 to 11, usually 10, n = 21; horizontal scale rows around caudal peduncle 12, n = 21.

Dorsal-limb gill rakers 5 to 6, either 5 or 6, n = 21; ventral-limb gill rakers 10 to 11, usually 11, n = 21.

Total number of vertebrae including Weberian apparatus and terminal compound centrum 32 to 34, usually 33, n = 30.

Dental Morphology. There is greater variation in tooth placement in *P. innesi* (Figs. 21–23) than in *P. simulans* or *P. axelrodi.* Géry (1960b: 9), noted the usual condition in wild-caught specimens as a slightly irregular series of six or seven tricuspid teeth (we find a rare count of eight), with one or more teeth offset somewhat anteriorly to other teeth of the row (Fig. 21A–D). The anteriorly-set teeth were interpreted by Myers (1936: 97) as a second row and by Géry (1960b: 9) as members of a "wavy" single tooth row. To determine whether either hypothesis should be rejected, we examined a large series of specimens, both wild caught and from the aquarium trade. Recently imported

TABLE 3. MORPHOMETRICS AND MERISTICS OF *Paracheirodon innesi*.†

	Holotype	Brazil, Amazonas (n = 1 or 0)	Colombia, Lago Yahuacaca				
			n	Range Low	Range High	$\bar{X}$	SD
Standard length	21.4	14.3	20	13.9	22.2	16.6	
Greatest body depth	35.0	28.0	20	22.7	28.8	26.2	1.392
Snout to dorsal-fin origin	54.2	53.0	20	49.7	54.7	52.6	1.092
Snout to pectoral-fin origin	27.1	31.5	20	28.4	32.5	30.7	1.014
Snout to pelvic-fin origin	49.5	51.7	20	45.5	50.0	47.7	1.099
Snout to anal-fin origin	64.0	62.2	20	56.2	63.1	61.1	1.581
Eye to dorsal-fin origin	37.4	36.4	20	33.0	37.5	35.3	0.960
Dorsal-fin origin to caudal-fin base	52.3	50.3	20	50.3	53.8	51.7	0.929
Caudal peduncle depth	10.7	9.8	20	8.8	10.6	9.8	0.467
Caudal peduncle length	16.4	17.5	20	14.8	18.0	16.0	0.784
Pectoral-fin length	17.8	—	20	17.8	20.3	19.1	0.739
Pelvic-fin length	16.8	—	20	15.8	18.8	17.3	0.775
Dorsal-fin base length	—	13.3	20	12.5	14.4	13.5	0.620
Longest dorsal-fin ray length	23.8	—	19	25.5	30.2	28.7	1.074
Anal-fin base length	23.4	24.5	20	24.1	26.5	25.2	0.666
Longest anal-fin ray length	25.7	—	19	22.7	25.6	24.7	0.692
Bony head length	28.0	28.7	20	27.0	29.9	28.6	0.905
Horizontal eye diameter	45.5	43.9	20	40.0	45.5	43.1	1.409
Snout length	18.2	19.5	20	15.9	20.9	18.7	1.174
Least bony interorbital width	29.1	31.7	20	26.7	34.7	29.1	1.998
Upper jaw length	36.4	31.7	20	29.4	34.9	31.9	1.676
Branched dorsal-fin rays	8	9	20	9	9	9	0.000
Branched pectoral-fin rays	12	11	20	11	13	11.8	0.550
Branched pelvic-fin rays	7	6	20	6	7	6.9	0.308
Branched anal-fin rays	17	17	20	16	18	17.5	0.889
Horizontal scale rows between dorsal fin and pelvic fin	9	—	20	9	9	9	0.000
Predorsal scales	10	—	20	9	11	10.0	0.549
Perforated lateral-line scales	9	—	29	3	6	4.6	0.940
Lateral series scales	33	—	20	30	33	31.3	0.933
Horizontal scale rows around caudal peduncle	12	—	20	12	12	12	0.000
Dorsal-limb gill rakers	5	—	20	5	6	5.5	0.513
Ventral-limb gill rakers	11	—	20	10	11	11	0.224
Vertebrae	33	—	29	32	34	33	0.267

† Holotype, USNM 102109; Lago Miua, Amazonas, Brazil, MZUSP 13256; Lago Yahuacaca, Colombia, USNM 216699. Standard length is expressed in mm. The next 16 measurements (through head length) are percentages of standard length. The next four measurements are percentages of bony head length.

aquarium specimens have tooth-row patterns like those of wild-preserved fishes, but some specimens kept in aquaria for several months or years develop tooth distribution irregularities (discussed below); this may be related to the flake-food diet of aquarium specimens, or it may be a factor of age.

We find most wild-preserved *P. innesi* to have one or two teeth offset slightly anterior to the main tooth row. In our sample of *P. innesi* from near Leticia, Colombia (USNM 216699 and MCZ 52156) the third tooth from the premaxillary symphysis is offset in about 70 percent of the specimens examined, the fourth tooth is offset in about 20 percent, and the second and fifth teeth each are offset in about 10 percent. Rarely, two teeth are offset on the same premaxillary bone. These two teeth usually are the second and fourth, or third and fifth from the symphysis.

Body size apparently is not correlated with the number of teeth offset from the main row.

We find, with rare, notable exceptions, that the anteriorly offset teeth lack developed main-row teeth posterior to them. Their replacement teeth are present either in series with other replacement teeth or offset slightly anterior to the replacement tooth row (Figs. 21A, 23B).

While in most cases an anteriorly offset tooth of *P. innesi* cannot be called a "true" outer-row tooth, we find that some individuals retain a degree of genetic lability regarding tooth rows. An example is a wild-preserved specimen 13.5 mm SL (from MCZ 52156) with six teeth on each premaxilla (Fig. 22) and with the third tooth from the symphysis on each bone offset slightly anteriorly and conical rather than tricuspid. While the tooth on the left side clearly has one cusp (Fig. 22), the tooth on the right side (not illustrated) has tiny lateral protrusions which may represent underdeveloped cusps. On the left premaxilla of this specimen all the tricuspid teeth have tricuspid replacement teeth posterior to them; the replacement tooth for the anterior conical tooth lies slightly anterior to the rest of the replacement tooth row and has a single, elongate cusp. On the right premaxilla, the tooth nearest the symphysis had just moved into a functional position when the fish was preserved and its base is not fully developed; the second tooth also has a partially-emplaced replacement tooth. The conical tooth has what may be a forming replacement tooth, represented by a tiny mineralized element, lying anterodorsal to the other parts of the replacement tooth row. The fourth tooth from the symphysis is a replacement tooth almost in its functional position, and the fifth tooth is a partially-formed tricuspid replacement tooth.

Two aquarium specimens examined also are pertinent to this discussion. A *P. innesi* specimen purchased as an imported wild specimen and raised to 25.7 mm SL shows a single conical tooth set somewhat anterior to the other premaxillary teeth, with a tricuspid tooth posterior to it (Fig. 23A,C). This conical tooth may be a worn tricuspid tooth about to be replaced by a newly formed tricuspid tooth, or it may be a true, if somewhat misshapen, conical tooth being replaced. The second specimen, which lived for about four years in an aquarium, exhibits extraordinary tooth morphology (Fig. 23B,D). The medial two and lateral two teeth are positioned as usual, but between them there is a series of one conical and five tricuspid teeth. Perhaps most important to our discussion is the presence of a conical tooth set anteromedial to the two normally placed lateral teeth. This conical tooth is fully formed and sharply pointed, not a worn-down tricuspid tooth as may be the case in the previously discussed specimen. Posterior to this conical tooth is a replacement tooth in its own trench, situated anterior to the other replacement teeth. This condition is that seen in *P. simulans* which has a true second tooth row (Fig. 21A,B,D). While it is doubtful that wild fishes ever reach the age of this particular specimen, and while abnormal habitat and/or diet might have been partially responsible for the very unusual tooth arrangement, this specimen does demonstrate that the genetic potential for a second premaxillary tooth row remains in *P. innesi*.

We conclude that while in most specimens there is a "wavy" premaxillary tooth line, the potential remains, in some specimens, for a second tooth row to develop. Teeth of the premaxilla are not replaced simultaneously, but at least one or two teeth seem to be replaced out of synchrony with others. The sample size available is insufficient to determine replacement patterns.

The maxillary teeth in *P. innesi* number two to three, usually three, with three cusps on each tooth (Figs. 21C,D; 23C,D). In the old aquarium-raised specimen discussed above (Fig. 23D), a single conical tooth is present on the maxilla somewhat distal to the tricuspid teeth. Other aquar-

ium-raised specimens have one to four, usually two, maxillary teeth (n = 16; 12.9–26.5 mm SL).

Dentary teeth in *P. innesi* usually number six to nine, with the more medial teeth tricuspid and those lying more laterally and posteriorly are conical. We found no statistically significant increase in tooth cusp number with increased body size. Figures 21F and 23E are representative of dentary tooth morphology.

Color Pattern. In life, *P. innesi* (Fig. 3) back dark olive brown with reticulate dark chromatophore pattern as described in more detail below under color in alcohol. Intense iridescent blue-green lateral stripe extends from skin over anterior infraorbital bones, over cornea of eye (usually concentrated dorsally), sparingly over cheeks, over opercle, and posteriorly to within one to three scales anterior to adipose-fin base. Blue lateral stripe broadest in area approximately between dorsal and pelvic fins. Dense stripe of dark chromatophores dorsal to blue lateral stripe, broadest in area between opercle and dorsal-fin origin. Broad stripe of loosely scattered dark chromatophores ventral to blue lateral stripe. Numerous erythrophores cover area extending to a point about on a vertical from dorsal-fin origin anteriorly, posteriorly over scales of caudal-fin base, dorsally to just ventral to blue lateral stripe (and with a few erythrophores to dorsum of caudal peduncle in some individuals), and ventrally to anal-fin base. Side in area immediately ventral to blue lateral stripe without erythrophores; width of this apigmented area broadest in disturbed individuals, very narrow in undisturbed fish. Area of fewer erythrophores immediately dorsal to anal-fin base; this area defined dorsally by narrow stripe of dark chromatophores extending to ventral border of caudal-fin base. Belly silvery white, reflecting light blue ventrally under some light conditions. Fins hyaline except for distinct white stripe along anterior anal-fin rays, concentrated between posterior unbranched ray and anterior branched ray; indistinct whitish area along anterior border of dorsal fin and small white area in center of adipose fin in some specimens.

Compared to *P. simulans*, *P. innesi* with a bluer lateral stripe which extends only to adipose fin, more red on flanks, less blue on eye and face, and a much more distinct white line on anal fin. See also color description of *P. simulans*.

Compared to *P. axelrodi*, *P. innesi* with less red on belly and flank area, a somewhat narrower blue lateral stripe which extends less far posteriorly, and a much more distinct white line on anal fin. See also life color description of *P. axelrodi*.

In alcohol, *P. innesi* (Fig. 27) with ground color light cream brown. Scale pocket margins of dorsum and ventrally successive lateral scale rows lined with dark brown chromatophores. Small brown chromatophores may be scattered within scale pocket areas defined by marginal chromatophores. Midlateral stripe extends posteriorly from just posterior to eye to near adipose-fin base, then either terminating or becoming abruptly less dense and continuing along dorsal half of caudal peduncle as far as squamation of caudal-fin base. Dorsal border of lateral stripe lies about two and a half scale rows ventral to dorsal-fin origin; maximum width of lateral stripe about one to two scales. Belly usually non-pigmented. Peritoneum with numerous dark chromatophores, more obvious in smaller specimens. Dark chromatophores lie along anal-fin base and along line marking conjunction of anal-fin musculature and hypaxial body musculature; these lines converge at posterior termination of anal-fin base. In some specimens, scale pocket margins along ventral midline of caudal peduncle with dark chromatophores. Large dark chromatophores on area of infraorbital 1 are probably an anterior continuation of lateral stripe. Numerous small dark chromatophores over tips of jaws and dorsum of head, these extending posteriorly as a diffuse thin line to caudal-fin base, marking

TABLE 4. SIMILARITIES AND DIFFERENCES AMONG DORSAL-LIMB GILL RAKER COUNTS OF POPULATION SAMPLES OF THREE SPECIES OF *Paracheirodon*.†

	n	Range		$\bar{X}$	SD	t	P
Comparison between:							
P. simulans, Puerto Correño	42	5	6	5.9	0.328	14.626	**
P. axelrodi, Tapurucuara	35	6	8	7.1	0.404		
P. simulans, Puerto Correño	42	5	6	5.9	0.328	7.638	**
P. axelrodi, Rio Morocoto	13	6	8	6.9	0.641		
P. simulans, Puerto Correño	42	5	6	5.9	0.328	7.742	**
P. axelrodi, Caño Muco	18	6	7	6.7	0.461		
P. simulans, Puerto Correño	42	5	6	5.9	0.328	3.526	**
P. innesi, Lago Yahuacaca	20	5	6	5.5	0.513		
P. innesi, Lago Yahuacaca	20	5	6	5.5	0.513	12.960	**
P. axelrodi, Tapurucuara	35	6	8	7.1	0.404		
P. innesi, Lago Yahuacaca	20	5	6	5.5	0.513	7.015	**
P. axelrodi, Rio Morocoto	13	6	8	6.9	0.641		
P. innesi, Lago Yahuacaca	20	5	6	5.5	0.513	7.560	**
P. axelrodi, Caño Muco	18	6	7	6.7	0.461		
P. axelrodi, Tapurucuara	35	6	8	7.1	0.404	3.215	**
P. axelrodi, Caño Muco	18	6	7	6.7	0.461		
P. axelrodi, Tapurucuara	35	6	8	7.1	0.404	1.272	NS
P. axelrodi, Rio Morocoto	13	6	8	6.9	0.641		
P. axelrodi, Caño Muco	18	6	7	6.7	0.461	0.999	NS
P. axelrodi, Rio Morocoto	13	6	8	6.9	0.641		

† Square-root transformations were used in computing the value of t. Two-tailed test; * indicates $P < 0.05$; ** indicates $P < 0.01$; NS (not significant) indicates $P > 0.05$.

dorsal midline. Small dark chromatophores line fin-ray borders; interradial membranes without chromatophores. Adipose fin with or without small dark chromatophores.

DISCUSSION

The most obvious differences among the neon tetras are expressed in the key to the species. Tables 4 to 7 express statistical differences and similarities in counts of the dorsal and ventral limb gill rakers, perforated lateral-line scales, and branched anal-fin rays among population samples of the three neon tetra species. These tables show highly significant count differences among the species and in some instances between population samples of *P. axelrodi*. Other counts, except those used in the key, were essentially the same. Differences in tooth patterns, color pattern, and orbital bones are described either in the key, the descriptions of the species, or both. *Paracheirodon simulans* has several morphometric characters which may distinguish it from the other two species. These are a proportionately shorter dorsal-fin base length (probably a factor of its fewer fin rays), a shorter longest fin ray in the dorsal fin, a relatively short anterior anal-fin lobe, a relatively longer upper jaw, shorter head length; also, the distance between the posterior border of the eye and the dorsal-fin origin is longer relative to the distance between the dorsal-fin origin and the caudal-fin base. Among these three species most of these characters overlap in their ranges. Although our analyses of these apparent differences have shown some to be significant, they are not presented here because our measurements of

TABLE 5. SIMILARITIES AND DIFFERENCES AMONG VENTRAL-LIMB GILL RAKER COUNTS OF POPULATION SAMPLES OF THREE SPECIES OF *Paracheirodon*.†

	n	Range		$\bar{X}$	SD	*t*	*P*
Comparison between:							
P. simulans, Puerto Correño	42	10	12	11.2	0.484	9.485	**
P. axelrodi, Tapurucuara	36	11	13	12.3	0.535		
P. simulans, Puerto Correño	42	10	12	11.2	0.484	9.943	**
P. axelrodi, Rio Morocoto	13	12	14	12.8	0.555		
P. simulans, Puerto Correño	42	10	12	11.2	0.484	9.234	**
P. axelrodi, Caño Muco	18	12	14	12.6	0.608		
P. simulans, Puerto Correño	42	10	12	11.2	0.484	2.529	**
P. innesi, Lago Yahuacaca	20	10	11	11.0	0.224		
P. innesi, Lago Yahuacaca	20	10	11	11.0	0.224	11.221	**
P. axelrodi, Tapurucuara	36	11	13	12.3	0.535		
P. innesi, Lago Yahuacaca	20	10	11	11.0	0.224	13.893	**
P. axelrodi, Rio Morocoto	13	12	14	12.8	0.555		
P. innesi, Lago Yahuacaca	20	10	11	11.0	0.224	11.608	**
P. axelrodi, Cño Muco	18	12	14	12.6	0.608		
P. axelrodi, Tapurucuara	36	11	13	12.3	0.535	1.700	**
P. axelrodi, Caño Muco	18	12	14	12.6	0.608		
P. axelrodi, Tapurucuara	36	11	13	12.3	0.535	2.914	**
P. axelrodi, Rio Morocoto	13	12	14	12.8	0.555		
P. axelrodi, Caño Muco	18	12	14	12.6	0.608	1.103	NS
P. axelrodi, Rio Morocoto	13	12	14	12.8	0.555		

† Square-root transformations were used in computing the value of *t*. Two-tailed test; * indicates $P < 0.05$; ** indicates $P < 0.01$; NS (not significant) indicates $P > 0.05$.

P. simulans are based mostly on juveniles and on adults raised in an aquarium. Because of possible growth aberrancy we only suggest that these differences should be investigated in the future with wild caught and preserved samples.

The above data and those presented in the key indicate that *P. axelrodi* and *P. innesi* share more characters with each other than either one or the other shares with *P. simulans*. However, it does not necessarily follow that *P. axelrodi* and *P. innesi* are sister taxa because many of the characters they share may be primitive. We were unable to establish the polarity of many of the traits since we have no precise outgroup hypothesis. An example is the orbital bones of the neon tetras (Fig. 28). The orbital series of both *P. axelrodi* (Fig. 28A) and *P. innesi* (Fig. 28B) includes a large third infraorbiral, a similarity. However, this is probably a primitive character for *Paracheirodon*, present in the ancestor of all three neon tetras. The loss of the bone in *P. simulans* may therefore represent an autapomorphy. Since autapomorphies and plesiomorphies are not informative about relationships, the similarity of the presence of the third orbital in *P. axelrodi* and *P. innesi* probably tells nothing about relationships among the three species. Likewise, other characters such as laterosensory canal reduction, fin length, body proportions, fin-ray numbers, and others cannot be used because we were unable to evaluate their polarity. We thus have been unable to determine confidently the relationships among the species of *Paracheirodon*.

There is one character which appears unique to *P. axelrodi* and *P. innesi* within the characiforms. In life these two species

TABLE 6. SIMILARITIES AND DIFFERENCES AMONG PERFORATED LATERAL-LINE SCALE COUNTS OF POPULATION SAMPLES OF THREE SPECIES OF *Paracheirodon*.†

	n	Range		$\bar{X}$	SD	*t*	*P*
Comparison between:							
P. simulans, Puerto Correño	20	0	5	2.6	1.569	8.717	**
P. axelrodi, Tapurucuara	26	5	8	6.5	0.762		
P. simulans, Puerto Correño	20	0	5	2.6	1.569	4.186	**
P. axelrodi, Rio Morocoto	7	5	7	6.0	0.577		
P. simulans, Puerto Correño	20	0	5	2.6	1.569	—	—
P. axelrodi, Caño Muco	1	6	6	6.0	—		
P. simulans, Puerto Correño	20	0	5	2.6	1.569	4.451	**
P. innesi, Lago Yahuacaca	20	3	6	4.6	0.940		
P. innesi, Lago Yahuacaca	20	3	6	4.6	0.940	7.333	**
P. axelrodi, Tapurucuara	26	5	8	6.5	0.762		
P. innesi, Lago Yahuacaca	20	3	6	4.6	0.940	3.424	**
P. axelrodi, Rio Morocoto	7	5	7	6.0	0.577		
P. innesi, Lago Yahuacaca	20	3	6	4.6	0.940	—	—
P. axelrodi, Caño Muco	1	6	6	6.0	—		
P. axelrodi, Tapurucuara	26	5	8	6.5	0.762	—	—
P. axelrodi, Caño Muco	1	6	6	6.0	—		
P. axelrodi, Tapurucuara	26	5	8	6.5	0.762	1.592	NS
P. axelrodi, Rio Morocoto	7	5	7	6.0	0.577		
P. axelrodi, Caño Muco	1	6	6	6.0	—	—	—
P. axelrodi, Rio Morocoto	7	5	7	6.0	0.577		

† Square-root transformations were used in computing the value of *t*. Two-tailed test; * indicates $P < 0.05$; ** indicates $P < 0.01$; NS (not significant) indicates $P > 0.05$.

have the blue lateral body stripe somewhat dorsal in position and terminating posteriorly in the vicinity of the adipose fin, rather than reaching the caudal-fin base as in *P. simulans*. In all other characids known to us the body stripe, when present, continues to the caudal-fin base. This character is unique to these species and therefore may represent a synapomorphy relating them.

Another character which may represent a synapomorphy for *P. axelrodi* and *P. innesi* is a short, or at least blunt, ascending premaxillary process (compare Figs. 19–23), as reported by Géry (1960b: 9, footnote). However, as reported by Géry and confirmed by us, several species of *Cheirodon* also have a short or blunt ascending premaxillary process. Our own personal bias is that the situation is convergent and that *Cheirodon* and *Paracheirodon* acquired this character independently, making it a synapomorphy for *P. axelrodi* and *P. innesi*. However, this view cannot be maintained until a more precise outgroup hypothesis is available.

We have been able to find only one character unique to *P. axelrodi* and *P. innesi*, slender evidence that they are sister taxa relative to *P. simulans*. We suggest that this problem should be the subject of future investigation.

SUMMARY

1) The systematics of the American Characidae are reviewed, and it is stated that phylogenetic analyses of the family eventually will produce considerable alteration in our understanding of the interrelationships of its member taxa and of their classification.

TABLE 7. SIMILARITIES AND DIFFERENCES AMONG BRANCHED ANAL-FIN RAY COUNTS OF POPULATION SAMPLES OF THREE SPECIES OF *Paracheirodon*.†

	n	Range		$\bar{X}$	SD	t	P
Comparison between:							
P. simulans, Puerto Correño	25	15	18	16.0	0.707	0.131	NS
P. axelrodi, Tapurucuara	48	15	19	16.0	0.841		
P. simulans, Puerto Correño	25	15	18	16.0	0.707	0.000	NS
P. axelrodi, Rio Morocoto	13	14	17	16.0	0.707		
P. simulans, Puerto Correño	25	15	18	16.0	0.707	0.813	NS
P. axelrodi, Caño Muco	18	15	17	16.2	0.618		
P. simulans, Puerto Correño	25	15	18	16.0	0.707	6.340	**
P. innesi, Lago Yahuacaca	20	16	19	17.5	0.889		
P. innesi, Lago Yahuacaca	20	16	19	17.5	0.889	3.835	**
P. axelrodi, Tapurucuara	48	15	19	16.6	0.841		
P. innesi, Lago Yahuacaca	20	16	19	17.5	0.889	5.137	**
P. axelrodi, Rio Morocoto	13	14	17	16.0	0.707		
P. innesi, Lago Yahuacaca	20	16	19	17.5	0.889	5.339	**
P. axelrodi, Caño Muco	18	15	17	16.2	0.618		
P. axelrodi, Tapurucuara	48	15	19	16.6	0.841	2.093	*
P. axelrodi, Caño Muco	18	15	17	16.2	0.618		
P. axelrodi, Tapurucuara	48	15	19	16.6	0.841	2.450	**
P. axelrodi, Rio Morocoto	13	14	17	16.0	0.707		
P. axelrodi, Caño Muco	18	15	17	16.2	0.618	0.698	NS
P. axelrodi, Rio Morocoto	13	14	17	16.0	0.707		

† Square-root transformations were used in computing the value of t. Two-tailed test; * indicates $P < 0.05$; ** indicates $P < 0.01$; NS (not significant) indicates $P > 0.05$.

2) The relationships and classification of the three known neon tetras, *Paracheirodon*, are reviewed and chosen as an example of the kinds of phylogenetic problems that will arise in the phylogenetic study of American characids.

3) The monophyly of *Paracheirodon* is documented by eight synapomorphic characters, including two aspects of live color pattern (presence of intense blue or blue-green lateral body stripe and dense red pigment restricted to region ventral to lateral stripe), preserved color pattern (brown or black chromatophores underlying and extending dorsal to lateral stripe), the dorsally placed attachment of the pterotic aponeurosis to the skull, a dorsal position of the posttemporal-supracleithrum joint, the dorsal position of the epioccipital bridge on the skull, the attachment of the ventral posttemporal ligament to the intercalar on the lateral surface of the pterotic bone, and the sharply dorsally turned supraoccipital profile combined with a slender body form.

4) Characters of dental morphology, laterosensory system, and karyology are discussed and, with our current understanding of characid phylogenetics, found to be uninformative about relationships of the species of *Paracheirodon*.

5) The three species of *Paracheirodon*, *P. simulans*, *P. axelrodi*, and *P. innesi* are diagnosed and differentiated.

6) The evidence for interrelationships of the species of *Paracheirodon* is discussed and one character, the dorsal placement of the lateral blue body stripe in life and its posterior termination near the base of the adipose fin, is found to be unique to two, *P. axelrodi* and *P. innesi*. We were unable to hypothesize polarities

for other characters common to any pair of the three species because all of the characters appear in at least some other possibly related taxa and because we were unable to hypothesize a precise outgroup.

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APPENDIX 1, SPECIMENS EXAMINED

The characid specimens in the following list formed the basis for the comparative comments and for outgroup comparisons. In nearly all cases it was possible to examine alizarin preparations. Additional alizarin preparations listed in Weitzman (1962) belong to the following species: *Aphyocharax alburnus* (Günther), *Astyanax fasciatus mexicanus* Filippi, *Brycon meeki* Eigenmann and Hildebrand, *Bryconamericus brevirostris* (Günther), *Bryconamericus ortholepis* Eigenmann, *Grundulus bogotensis* (Humboldt and Valenciennes), *Hemigrammus nanus* Lütken, *Hemigrammus unilineatus* Gill, and *Tetragonopterus argenteus* Cuvier. Three species of *Cheirodon*, listed in Fink and Weitzman (1974), were examined, *C. affinis* (Meek and Hildebrand), *C. dialepturus* Fink and Weitzman, and *C. terrabae* Bussing.

There were species in some genera, e.g., *Tyttobrycon* Géry, which we were not able to examine. Comparison of these with *Paracheirodon* awaits new collections and further studies. Many other species in the genera listed below or in other genera were examined, mostly from specimens that were not alizarin preparations. Those listed below were selected to be examined in detail for a variety of reasons. Most are morphologically representative of the genera to which they have been assigned by past authors.

Aphyodite sp.—2 alizarin preparations, SL 22.1–11.7 mm, USNM 221932, Brazil, Amazonas, Lago Hyanuary (=Janauarí) (30°13′S, 60°9′W), near Manaus, Thayer Expedition, Major Coutinho, November–December 1865. [Dick, 1977, Figure 10 shows Lago Hyanuary (now spelled Janauarí) to be along the northeastern side of the Rio Negro northwest of Manaus. Lago Janauari lies south of Manaus on the neck of land between the confluence of the Rio Negro and the Rio Solimões. Mrs. Agassiz (Agassiz and Agassiz, 1868: 253) states that the lake is on the west side of the Rio Negro. Currently a lake with this name lies on the opposite side of the Rio Negro from Manaus, to the southwest.]

Astyanax fasciatus mexicanus (Filippi).—3 alizarin preparations, SL 37.5–60.3 mm, from 19 spms, MCZ 41365, Mexico, Tamaulipas, Río Guayalejo (approximately 23°0′N, 98°50′W), W. A. McLane and N. Marshall, December 1939.

Axelrodia riesei Géry.—6 alizarin preparations, SL 15.2–17.6 mm, USNM 221681, from 20 spms, USNM 231821, Colombia, Vaupés, Río Vaupés at Mitú (1°7′N, 70°4′W), H. R. Axelrod, November 1964.

Brittanichthys axelrodi Géry.—2 alizarin preparations, SL 19.8–22.2 mm, USNM 221682, Colombia, Vichada, Río Orinoco basin, Río Muco 50 km west of San Jose de Ocume (4°14′N, 70°50′W), R. Socolof, 3–5 July 1974.—17 alizarin preparations, SL 15.3–24.1 mm, USNM 221992, from 60 spms, USNM 221991 (also 60 spms at MZSUP), Brazil, Amazonas, Rio Negro drainage, near mouth of Rio Urubaxi (0°24′S, 65°2′W), M. Goulding, 11 February 1980.

Bryconamericus meridae (Eigenmann).—4 alizarin preparations, SL 25.9–39.2 mm, USNM 221933, from 193 spms, USNM 121469, Venezuela, Trujillo, Maracaibo basin, Río Motatán, 4 km above Motatán (9°19′N, 70°35′W), L. P. Schultz, G. Zuloaga, W. H. Phelps Jr., 15 March 1942.

Bryconella pallidifrons (Fowler).—1 holotype of *Cheirodon pallidifrons* Fowler, SL 22.8 mm, ANSP 71728, aquarium spm donated 3 July 1940 by J. L. Troemner.—1 holotype of *Hyphesssobrycon thompsoni* Fowler, SL 18.4 mm, ANSP 71849, aquarium spms donated March 1949 by H. E. Thompson.—6 spms, SL 21.4–27.4 mm, USNM 216205, aquarium spms imported with *Paracheirodon innesi*, 1976, probably from near Leticia, Colombia.—4 alizarin preparations, SL 19.0–27.4 mm, USNM 221676, same data as USNM 216205.—5 spms, SL 18.8–20.7 mm, MCZ 52163, Colombia, Amazonas, Río Marañon, several km upriver from Leticia, small stream flowing into Lago Yahuacaca (4°6′S, 69°58′W), W. L. Fink, 3 December 1976.—2 spms, SL 18.2–18.5 mm, USNM 216701, same data as MCZ 52163.

Characidium sp.—2 alizarin preparations, SL 27.8–35.5 mm, USNM 222017, from 68 spms, USNM 222017, Colombia, Vichada, Río Orinoco basin, Caño Muco, 50 km west of San Jose de Ocume (4°14′N, 70°50′W), R. Socolof, 3–5 July 1974.

Cheirodon australe Eigenmann.—2 alizarin preparations, SL 32.1–46.4 mm, USNM 221998, from 14 paratypes, USNM 84317, Chile, Llanquihue, creek flowing into Lago Llanquihue at Puerto Varas (41°20′S, 72°68′W), C. H. Eigenmann, 12 March 1919.

Cheirodon galusdae Eigenmann.—2 alizarin

preparations, SL 30.6–52.1 mm, USNM 221997, from 11 paratypes, USNM 84319, Chile, Talca, Río Loncomilla (=Río Locomilla of Eigenmann) at San Javier (=San Xavier of Eigenmann) (35°35′S, 71°44′W), C. H. Eigenmann, 23 March 1919.

Cheirodon interruptus (Jenyns).—16 alizarin preparations, SL 14.0–33.9 mm, USNM 221674, from 107 spms, USNM 221673 (an equal number of spms at MZUSP), Brazil, Rio Grande do Sul, Município de Rio Grande, Arroio Senandes where it crosses road between Rio Grande and Cassino (32°09′S, 52°11′W), N. Menezes, L. Chao, S. Weitzman, M. Weitzman, and L. Jardim, 10 December 1979.—3 alizarin preparations, SL 19.8–40.6 mm, from 36 spms, FMNH 50629, Uruguay, Minas, Arroyo Polanco (33°56′S, 55°20′W), tributary to Río Cebollati, C. C. Sanborn, December 1926.

Cheirodon piaba Lütken.—3 alizarin preparations, SL 18.0–22.7 mm, from 17 spms, FMNH 50136, Brazil, Paraná, Rio Itararé (24°7′S, 49°20′W) a town on Rio Itararé, tributary to Rio Paranapanema, E. R. Blake, September 1937.

Cheirodon pisciculus Girard.—1 alizarin preparation, SL 52.3 mm, USNM 221996, from 9 spms, USNM 84316, Chile, Valparaiso, Río Aconcagua at La Calera (32°47′S, 71°12′W), C. H. Eigenmann, 13 April 1919.—2 alizarin preparations, SL 39.2–41.5 mm, from many spms, CAS 20655 (IUM 15504), Chile, Santiago, Río Maipo basin Río Angustura at Hospital (33°52′S, 70°55′W), C. H. Eigenmann, 22 April 1919.—1 alizarin preparation, SL 28.6 mm, USNM 222009, from 9 spms, USNM 84318, same locality data as CAS 20655.

Elachocharax geryi Weitzman and Kanazawa.—1 alizarin preparation, SL 12.5 mm, USNM 215288, Colombia, Vichada, Río Orinoco basin, Caño Muco (between 4°14′N, 70°2′W and 4°58′N, 71°58′W), a tributary to Río Vichada, J. E. Thomerson, D. L. Hicks, and J. H. Vaques, 24 April 1974.

Gymnocorymbus thayeri Eigenmann.—1 alizarin preparation, SL 27.5 mm, CAS(IUM) 15881, Peru, Loreto, brooks and ponds at Iquitos (3°45′S, 73°12′W), W. R. Allen, September 1920.

Hemigrammus erythrozonus Durbin.—1 lectotype, SL 23.4 mm, FMNH 53546, Guyana (=British Guiana), Essequibo, Erukin Creek (5°18′N, 59°16′W), lower Potaro River, C. H. Eigenmann, 30 October 1908.—5 spms, "paralectotypes," SL 21.1–23.3 mm, CAS(IUM) 11905, same data as FMNH 53546.—5 alizarin preparations, SL 22.9–32.5 mm, USNM 216709, aquarium spms, December 1976.

Hemigrammus levis Durbin.—4 alizarin preparations, SL 17.0–41.6 mm, USNM 221938, from 28 spms, USNM 221937, Brazil, Amazonas, Rio Negro basin, Rio Jufari (=Rio Tupari), between Santa Fe and Castanheiro Grande (mouth of Rio Jufari is at 1°23′S, 62°0′W), M. Brittan, 21 April 1964.

Hemigrammus pulcher Ladiges.—3 alizarin preparations, SL 19.0–23.1 mm, USNM 221936, Colombia, Amazonas, Leticia (4°13′S, 69°56′W), D. Kramer, 4 December 1974.

Hemigrammus rhodostomus Ahl.—1 alizarin preparation, SL 29.1 mm, USNM 222018, from 5 spms, USNM 94305, Brazil, Pará, Ilha de Arapiranga (no specific site designated), 1934. These specimens were discussed by Myers in Eigenmann and Myers (1929: 352).

Hemigrammus sp.—16 alizarin preparations, SL 13.6–30.4 mm, USNM 221671, from 99 spms, USNM 221672, Brazil, Pará, Rio Marituba at Marituba (1°25′S, 48°15′W), B. B. Collette, 23 May 1975.

Hyphessobrycon compressus (Meek).—1 alizarin preparation, SL 30.7 mm, USNM 204387, from 3 spms, FMNH 4642, Mexico, Oaxaca, El Hule, S. E. Meek, 22 April 1903.

Hyphessobrycon sp.—18 alizarin preparations, SL 13.1–25.9 mm, USNM 221679, from 147 spms, USNM 221680, Brazil, Pará, Rio Ihangapi at Ihangapi (0°9′S, 47°9′W), B. B. Collette, 23 May 1975.

Hyphessobrycon loretoensis Ladiges.—8 alizarin preparations, SL 13.9–20.3 mm, USNM 221675, from 42 spms, USNM 216700, Colombia, Amazonas, Rio Loreto-Yacu (3°30′S, 70°10′W), N. Navarro C., November 1976.

Hyphessobrycon lütkeni (Boulenger).—15 alizarin preparations, SL 11.9–37.1 mm, USNM 221677, from 204 spms, USNM 221678 (an equal number of spms at MZUSP), Brazil, Rio Grande do Sul, southeast of Pôrto Alegre, Município de Viamão, small tributary of Rio Fiuza along Paso Comprido, N. Menezes, S. Weitzman, and M. Weitzman, 9 December 1979.

Klausewitzia aphanes Weitzman and Kanazawa.—2 alizarin preparations, SL 14.8–14.9 mm, USNM 221995, from 14 spms, USNM 213783, aquarium spms imported with *Paracheirodon axelrodi* from Manaus, Brazil, probably collected during 1975 from "upper Rio Negro."

Leptobrycon sp.—1 alizarin preparation, SL 21.7 mm, USNM 222013, from 4 spms, USNM 222012, Venezuela, Amazonas, Río Atabapo (4°3′N, 67°43′W), tributary to Rio Orinoco, A. Cortez, J. O. Silva, 23 February 1974.

Microschemobrycon casiquiare Böhlke.—2 alizarin preparations, SL 25.1–25.3 mm, from 29 spms, CAS(SU) 17511, paratypes, Brazil, Amazonas, Rio Negro at Cucuy (=Cucuhy) (1°12′N, 66°50′W), C. Ternetz, 14 February 1925.

Microschemobrycon sp.—8 alizarin preparations, SL 25.1–30.8 mm, USNM 221911, from 33 spms, USNM 221912 (25 spms at MZUSP), Brazil, Amazonas, Rio Aripuanã, tributary of Rio Madeira (5°8′S, 60°24′W), H. Britski, N. Menezes, 7 November 1976.

Neolebias olbrechtsi (Poll).—2 alizarin preparations, SL 22.0–23.8 mm. USNM 222015, Zaire, stream flowing into Lake Tumba near Bikoro, collector and date unknown.

Oxybrycon sp.—1 alizarin preparation, SL 14.1 mm, CAS(SU) 47192, Brazil, Amazonas, Rio Negro at Cucuy (=Cucuhy) (1°12′N, 66°50′W), C. Ternetz, 14 February 1925.

Parecbasis cyclolepis Eigenmann.—1 spm, SL 53.5 mm, ANSP 144104, Peru, Maynas, vicinity of Iquitos

(3°45'S, 73°12'W), Rio Nanay, Catherwood Expedition, 14 October 1945.

Pristella sp.—2 alizarin preparations, SL 28.9–33.8 mm, USNM 222008, from 6 spms, USNM 66267, Guyana (=British Guiana), trenches, Botanic Gardens at Georgetown (6°47'N, 58°10'W), S. E. Shidler, September 1908,—2 alizarin preparations, SL 17.2–22.1 mm, USNM 222011, from 6 spms, USNM 222010, Surinam, Pará, 43 km south of Paramaribo, blackwater creek near islands, Bosbeheer HQ at Zanderij, D. W. Dunham, 9 April 1969.

Thrissobrycon pectinifer Böhlke.—1 alizarin preparation, paratype, SL 24.0 mm, CAS(SU) 16945, Colombia, Vaupés, Rio Negro, "from a sand bank on the Colombian border," C. Ternetz, 14 February 1925.

Tyttocharax madeirae Fowler.—6 alizarin preparations, SL 13.5–17.9 mm, USNM 222007, from 52 spms, USNM 179540, Brazil, Amazonas, Rio Urubú, "about 25 km from Itacoatiara (3°7'S, 58°39'W), H. Schultz, October 1958.

APPENDIX 2, TYPE LOCALITIES OF SPECIES OF *PARACHEIRODON*

All of the neon tetras, as originally described, were accompanied by erroneous or vague locality information. The following account is offered to bring the record up-to-date.

Myers (1936: 97) listed the type locality of *P. innesi* as follows. "It formed part of an importation obtained by a French collector of aquarium fishes from the Peruvian Amazon; it was received by Mr. Innes directly from the importer in Paris for identification, together with information making it seem likely that the locality was near Iquitos." Subsequently Innes (1936) published an account of the introduction of *P. innesi* into the aquarium trade, making it clear that the holotype (USNM 102109) is a specimen from the original importation sent to Paris in 1936 from South America. Stoye (1936) published an article about the discovery of *P. innesi* based on an interview with August Rabaut, the collector. The fishes were taken in March and/or April 1936 during a trip by canoe traveling up the Rio Putumayo into the State of Amazonas, Colombia. The precise locality in this region is not recorded and the specimens may have been obtained from several localities. Since then many millions of neon tetras have been exported from the areas of Peru and Colombia adjacent to the Rio Putumayo and from areas in Peru, Colombia, and Brazil adjacent to Tabatinga and Leticia. Ladiges (1973, 1978, and 1979) provided information on the discovery of *P. innesi*. Geisler (1979) published an account of collecting *P. innesi* in the Rio Curaray, a tributary of the Rio Napo in Peru.

It was not until 1960 that specimens with exact locality data found their way into the scientific community (Géry, 1965a: 31). These specimens were from the Igarapé Prêto near the little village of Belém, Amazonas, Brazil, about 60 km downstream on the Rio Solimões from the border region between Brazil, Colombia, and Peru. The only other specimens with locality data known to us are those reported here.

The history of the discovery of *P. axelrodi* is more complex than that of *P. innesi* or *P. simulans*, but its distribution now seems clear. *Paracheirodon axelrodi* was described nearly simultaneously by Schultz (1956) and by Myers and Weitzman (1956). These two sets of authors recorded different type localities. Schultz (1956: 42) reported his two specimens as being from somewhere near Pôrto Velho [on the Rio Madeira], Amazonas, Brazil. At the end of Schultz's description (p. 43) the editor appended a short note that the specimens used in the description were supplied by H. R. Axelrod who obtained them from Sol Kessler of the Fish Bowl, New Jersey. Axelrod (1956: 16) reported that this species was brought to his attention on February tenth or eleventh by several of his friends and that specimens received from Mr. Kessler were the ones sent to Schultz at the Smithsonian Institution for identification. Axelrod (1956: 17) further reported that he was unable to get information on the collecting locality of *P. axelrodi* from the importers, Fred Cochu and Mr. Schnelle of Paramount Aquarium Inc., but that the locality information he did get came from a person

(unnamed) who formerly collected fishes in the region where these fishes are found. Axelrod (1956: 17) stated that this person told him that this species came from north of Pôrto Velho on the Rio Madeira.

Myers and Weitzman (1956: 1) gave as their type locality for *Hyphessobrycon cardinalis* (=*P. axelrodi*), "Rio Negro, Amazonas, Brazil." They reported receiving their specimens and locality information from Paramount Aquarium Inc. through W. T. Innes. They recorded more complete information on the label in the bottles (SU 48710, holotype, and SU 48711, eleven paratypes and SU 48712, 2 alizarin specimens, all now at CAS) as Tomar (0°25′S, 63°55′W) on the Rio Negro, State of Amazonas, Brazil, collected in the winter of 1955–1956. This more precise information was supplied by Paramount Aquarium Inc., but its publication was withheld at their request. Weitzman (1956: 257–258) provided some history of the discovery of *P. axelrodi*, citing Ladiges (1956) as a source. Weitzman noted that this fish is from the Rio Negro, not the Rio Madeira and that Ladiges (1956) stated that in 1953 he received a letter from Prof. Harold Sioli, a well known German limnologist studying the river systems of the Amazon basin, stating that in September of 1952 he (Sioli) found a neon tetra near the mouth of the Rio Uaupes (=Vaupés in Colombia) and the Rio Içana near São Felipe. Both streams are tributaries from the west to the Rio Negro with their headwaters in Colombia.

In February of 1979 one of us (Weitzman) discussed this discovery with Professor Sioli who later provided the following information derived from his field notes for 1952. "In the fall of 1952 I made a trip to the upper Rio Negro together with some colleagues of the Instituto Agronomico do Norte, Belém and Prof. Theodosius Dobzhansky. On September 24, 1952 I collected hydrobiological material in front (river side) of Içana (formerly São Felipe) near Sitio Caburis. I looked into a very small forest pond, less than one meter wide and deep, and among the dead leaves on the bottom I suddenly saw in the brown water some silvery double-points [eyes with silvery pigment over their dorsal surface]. I quickly dipped my net into the water and caught some beautiful-coloured fishes, red and blue, which I, as a non-ichthyologist, thought to be the neon tetra, *Hyphessobrycon innesi*. I only wondered to find that species so far distant from the area around Leticia on the upper Solimões river, from where the fish is commonly exported for aquarium hobbyists." Prof. Sioli preserved and labeled a few specimens with locality information and later (1953) sent them to Dr. Ladiges, then at the Zoological Institute of the University of Hamburg. Apparently the fish were lost in the mail, for Ladiges never received the specimens. Prof. Sioli also noted that he mentioned this discovery to Dietrich Horie of Belém, who at that time organized the fishing expeditions for Mr. Cochu of Paramount Aquarium Inc., New York.

In retrospect, it might now appear that Prof. Sioli could have collected either *P. axelrodi* or *P. simulans*; however, one of us (Weitzman) interviewed the aquarium fish collector and exporter H. Willi Schwartz of Manaus, Brazil in 1977 concerning the habitats and collecting sites of *P. axelrodi* and *P. simulans*. The two species appear to have the same or at least partly the same geographical range. Mr. Schwartz reported that *P. axelrodi* is ordinarily found in the lower portions of the streams tributary to the upper Rio Negro, while *P. simulans* occurs upstream and rarely, if ever, are the two species found at the same location. This would make it seem very probable that Sioli actually captured *P. axelrodi* since he captured his specimens near the Rio Negro.

Axelrod (1976 and 1980) has published accounts of the discovery of *P. axelrodi* differing from that reported above.

Paracheirodon simulans was described by Géry (1963) and the types were stated to have been collected by H. W. Schwartz

from the Rio Purus during November of 1962. Géry (1966c: 231) corrected this locality to the Rio Jufaris (or Tupari), which empties into the Rio Negro near the mouth of the Rio Branco. The correction was supplied to Géry by the collector, H. W. Schwartz.

Citing aquarium collectors as his source, Géry (1966c: 231–232) discussed the distribution of the neon tetras. The records we include above considerably expand the locality information provided by Géry for *P. axelrodi* and especially for *P. simulans*. Géry (1966c: 232) stated that *P. innesi* is present along the Rio Solimões from São Paulo de Olivença in Brazil and along the Rio Marañon (the name for the Rio Solimões in Peru) up to Iquitos in Peru. We have no information for the existence of *P. innesi* in that region of the Rio Marañon but have no reason to doubt this possibility. Kullander's report, noted here under the species description of *P. innesi*, of specimens from the lower Rio Ucayali in Peru would seem to confirm Géry's report and to extend the range somewhat.

APPENDIX 3, COMMENTS ON CHARACTERS CURRENTLY PHYLOGENETICALLY UNINFORMATIVE

Three character systems, the dental morphology, the laterosensory system, and karyology commonly vary in characids and, at least in the first two, are easily accessible for morphological and systematic investigation. These have been used frequently in the past to assess relationships among characids. As explained below, we have serious doubts about the current use of these characters. We are certain that these characters are phylogenetically significant at some of the various taxonomic levels in the characids that have them. At other levels they probably represent homoplasies. We have been unable to evaluate their phylogenetic appropriateness for *Paracheirodon*. This is because of the widespread but sporadic occurrence of these characters in many characids and because of our failure to find specific outgroups for *Paracheirodon*. It is our view that caution is necessary in utilizing the characters discussed below. One should not propose hypotheses of relationship beyond the limits of homology (synapomorphy) established by a combination of the study of morphological similarity, the application of outgroup comparison, and the determination of a parsimonious distribution of characters among the studied taxa. Our viewpoint about the use of ontogeny in the assessment of character polarity is discussed by Fink (1982).

Since these characters have been applied by others, as explained below, to questions of relationship about the species we place in *Paracheirodon*, we find it useful to discuss them at this point.

Dental Morphology. This character "complex" historically has been one of the most important in characid classification. Numbers of tooth rows on the premaxillae define "subfamilies," e.g.: two tooth rows, Tetragonopterinae, Eigenmann (1917: 38–43); one row, Cheirodontinae, Eigenmann (1915: 3–10). In combination with other characters, numbers of teeth in the premaxillary rows define genera. For example, there are five inner row premaxillary teeth in *Astyanax* and four teeth in *Bryconamericus*. Consideration of relationships based on interpretations of tooth morphology has been the primary source of the "neon tetra problem." In the absence of synapomorphies diagnostic of *Paracheirodon*, *P. axelrodi* and *P. innesi* would be "cheirodontine" (in different genera) and *P. simulans* "tetragonopterine." Our assessment that these three species form a monophyletic group forces a reconsideration of dental morphology, specifically as applied to the problem of interrelationships within *Paracheirodon*. Unfortunately, our lack of a precise hypothesis of outgroups prevents us from utilizing such similarities as are present in the group. For example, *P. simulans* (Fig. 19A–D) has two rows of premaxillary teeth while *P. axelrodi* (Fig. 20A–D) and *P. in-*

nesi (Fig. 21A-D) have one row. If we find that there are two rows in the outgroup, the single row would be synapomorphous for the *axelrodi-innesi* pair. If, on the other hand, there is a single row in the outgroup, the two rows of *P. simulans* is an autapomorphy. Likewise, the analysis of tooth-cusp number: adult *P. simulans* have six to nine cusps on the large jaw teeth, adult *P. axelrodi*, five to seven, and adult *P. innesi*, three. Two alternative subgroups are possible, one based on cusp reduction (*P. axelrodi-P. innesi*), and the other on a cusp increase (*P. axelrodi-P. simulans*). Again, lack of an appropriate outgroup prevents use of these similarities.

We must admit that our personal biases suggest that the single tooth row and reduced cusp number are derived characters for *Paracheirodon*. The supposition regarding the former character is in part based on our observation (discussed in the Description Section) that *P. innesi* of advanced age occasionally develop a second tooth row (Fig. 23A–D). Nevertheless, our biases are unsupported by solid evidence and must be left out of the analysis.

Laterosensory System, Cranium, Pectoral Girdle, and Associated Structures. Laterosensory system reduction in *Paracheirodon* is extensive on both the head and body and formed part of the basis for the discussion of the relationships of *P. axelrodi* and *P. innesi* by Géry (1960b: 8–13). Laterosensory reductions in the postocular skull region were illustrated by Géry (1960b: 10–11, Figs. 6–8). In comparing his drawings with our cleared and stained specimens of these species we found a variety of discrepancies. Before proceeding with our own discussion of this region we find it appropriate to review Géry's efforts. Géry (1960b) noted that *P. innesi* and *P. axelrodi* have this region "comparable" (p. 9) and "the same" (p. 11). But on page 12 he stated: "Compared to *Cheirodon axelrodi* these structures [in *P. innesi*] (in particular the circumorbital and otic series) make believe [sic] that the two forms [*P. axelrodi* and *P. innesi*] which are also extremely similar, have evolved independently from a common cheirodontine ancestor and probably recently." This statement seems to indicate that Géry detected differences in this region which, along with those he found in the jaws, prompted him to hypothesize convergence of external characters such as color pattern for these two fishes. However, Géry's illustrations (Fig. 7) of the postocular skull of these two neon tetras show some rather drastic differences in the bones he labelled as epiotic, supratemporal, and posttemporal. Upon comparison of Géry's illustrations with the specimens at hand, we find a considerable amount of error in both his drawing and labeling. Compare Géry's illustrations with Figures 4, 5, 7 of *P. axelrodi* and 8 of *P. innesi* in the present paper and note their similarity to Figure 6 of *P. simulans*. In both of Géry's illustrations the bone labeled as the cleithrum is the supracleithrum and that labeled as the supracleithrum is the posttemporal. In both illustrations Géry divided the frontal into two parts, labeling the anterior part the frontal and the posterior part the parietal. In both drawings he illustrated a supraorbital, a bone we found absent in all our cleared and stained specimens of *P. axelrodi* and *P. innesi* and in all "tetragonopterine" characids examined. The epioccipital (=epiotic) is not illustrated in his drawings. In his drawing of *P. innesi* he divides the parietal into two parts, labeling one the epiotic and the other supratemporal. In his drawing of *P. axelrodi* he divides the pterotic into two bones, labeling one the supratemporal and the other the pterotic. The exoccipital, epioccipital (=epiotic), and basioccipital bones are not present in Géry's drawings. He labels the parietal as the epiotic. With these kinds of errors in morphological representation we can place little confidence in Géry's statements about relationships based on his observations.

Reductions of the laterosensory portions of the postocular cranium and shoulder girdle are as follows. Laterosensory canals

are absent from all of the postocular cranial bones except the frontal (Figs. 4–8). The primitive laterosensory canal arrangement for characids is illustrated in Figures 9, 28A, 29 for *Astyanax* and Figures 10, 30 for *Gymnocorymbus*. Canal terminology used here follows Weitzman (1962: 65, Fig. 9). There are supratemporal and parietal canals in the parietal bone, a pterotic canal in the pterotic, all of which are absent in the species of *Paracheirodon* and, to varying degrees, in many small characids. *Cheirodon interruptus* (Fig. 11) shows relatively little laterosensory canal loss, whereas *Hemigrammus erythrozonus* (Fig. 12) shows considerably more. *Axelrodia riesei* (Fig. 13), *Brittanichthys axelrodi* (Fig. 14), and *Tyttocharax madeirae* (Fig. 15) have cranial laterosensory canal loss about equivalent to that of the neon tetras. The pygmy species of the Characidiinae, *Klausewitzia aphanes* (Fig. 17) and *Elachocharax geryi* (Fig. 18) also show much laterosensory canal loss.

The pterotic branch of the frontal laterosensory canal is absent in the neon tetras (Figs. 6–8). This branch is illustrated in its most extensive form in Figures 10, 30 of *Gymnocorymbus*. The canal is absent from the bone in *Astyanax* (Fig. 9) but is present in the skin over its surface (Fig. 29). The pterotic branch of the frontal canal is often reduced or lost in paedomorphic characids (Figs. 11–15, 18).

The neon tetras lack the extrascapular bone and its canal (Figs. 6–8). The primitive arrangement of the extrascapular bone with three openings and the laterosensory system is shown in Figures 9, 29 of *Astyanax* and Figures 10, 30 of *Gymnocorymbus*. The extrascapular is also absent in *Axelrodia* and *Brittanichthys* (Figs. 13, 14 respectively) and reduced in *Klausewitzia* (Fig. 17). In Figure 15 of *Tyttocharax* the small bone shown at the dorsal end of the supracleithrum is a posttemporal, not an extrascapular.

The posttemporal and supracleithrum are without laterosensory canals in the species of *Paracheirodon*. The primitive characid distribution of these canals is represented by *Astyanax* (Figs. 9, 29) and *Gymnocorymbus* (Figs. 10, 30). The canals are present in *Cheirodon interruptus* (Fig. 11) and *Hemigrammus erythrozonus* (Fig. 12), but absent in *Axelrodia riesei* (Fig. 13), *Brittanichthys axelrodi* (Fig. 14), and *Tyttocharax madeirae* (Fig. 15).

A suprapreopercular bone is absent in *Paracheirodon*. The bone is present in *Astyanax* (Fig. 9) and *Gymnocorymbus* (Fig. 10) as a tube bone dorsal to the preopercle and illustrated in the same pattern. The suprapreopercle is commonly absent in small characids (Figs. 11–18) and may be the first part of the head laterosensory system to be lost in small characids.

Other segments of the laterosensory system absent in *Paracheirodon* are the posterior infraorbitals and their canals of the circumorbital series (Fig. 24A–C).

The terminology we believe suitable for the circumorbitals was defined by Weitzman (1962: 28–31, Fig. 9). The term lachrymal, still extensively used in teleosts for the first (anterior) infraorbital, was excluded from consideration because there is no evidence of the homology of the bone with the lachrymal of non-teleostean vertebrates. Also, the terms "great suborbital" and "second suborbital," used for characids by Eigenmann in his extensive series of papers, is here called the third infraorbital. The bone is not a true suborbital as explained by Weitzman (1962: 28, footnote), and it is not the second bone in the infraorbital series. Terms such as suborbital and postorbital are used in several fossil fish groups for orbital bones which do not border the eye, and these orbital bones are not homologous with the infraorbital bones which do border the eye.

The antorbital is the most anterior element of the orbital series illustrated in Figures 4, 5, 28A,B. It lacks a laterosensory canal, lies in the posterolateral wall of the nasal capsule, and is dorsal to the first infraorbital.

The infraorbitals are numbered consec-

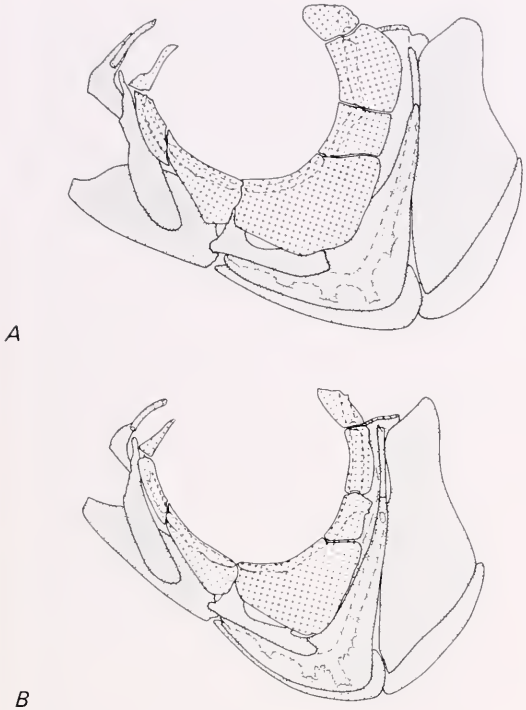

Figure 28. Face bones of three neotropical characids. Circumorbital bones represented by plus-sign (+) pattern. Lateral view, left side. A. *Astyanax fasciatus mexicanus,* SL 40.4 mm, MCZ 52104. B. *Gymnocorymbus thayeri,* SL 38.5 mm, MCZ 49962. C. *Hemigrammus erythrozonus,* SL 24.2 mm, USNM 216709.

utively, the anterior one being referred to as the first and the posterodorsal one as the sixth. The third infraorbital is the largest and apparently primitively has its ventral and posterior border along the pre-

Figure 29. Posterior region of skull and pectoral girdle of *Astyanax fasciatus mexicanus,* female, SL 52.4 mm, MCZ 41365, lateral view, left side. Distribution of laterosensory system illustrated by dense black dots.

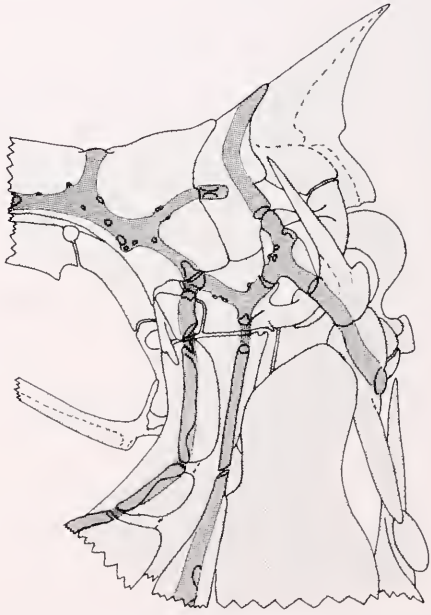

Figure 30. Postocular region of skull and pectoral girdle of *Gymnocorymbus thayeri,* adult, SL 27.5 mm, CAS(IUM) 15881, lateral view, left side. Distribution of laterosensory system illustrated by dense black dots.

opercular laterosensory canal (Weitzman, 1960: 64, Fig. 8). In many characids the third infraorbital is reduced in size so that its distal border (that away from the eye) does not contact the border of the preopercular canal (Fig. 28A–C). All infraorbital bones have laterosensory canals in relatively primitive characids. The supraorbital is apparently absent in "tetragonopterine" characids but is present in *Brycon* and some other characids such as *Serrasalmus*.

Reductions or absence of infraorbital four, five, and six (Figs. 11–18, 28C), and reductions in perforated lateral-line scales are of common occurrence in small and medium sized characids. These characters, also found in *Paracheirodon*, have evolved repeatedly through paedomorphosis and may be labile, subject to being phenotypically reacquired through heterochrony. Such characters, although certainly phylogenetically significant at some level, in practice are difficult to use as synapomorphies. Although the laterosensory reductions present in the neon tetras may help define *Paracheirodon*, we find it impossible to use them until we have a precise hypothesis of outgroup relationships.

Karyology. A survey of the literature of fish systematics (and of many other groups) for the past two decades shows an increasing use of chromosome number and morphology as characters. We expect to see the use of chromosome data increase with the continued refinement and simplification of karyological methods. Chromosome features, like any other characters, must be subject to phylogenetic analysis. Phenetic similarity or simple possession of similar numbers of chromosomes or arms does not necessarily indicate close relationship. We know of very few attempts to interpret karyotypic data in fishes in the phylogenetic paradigm, at least at lower taxonomic levels (e.g., Wiley and Hall, 1975). Farris (1978) has discussed analysis of chromosomes in phylogenetic inference.

In the problem at hand, we find the available data flawed. Attempts to date to characterize the karyotypes of *P. axelrodi* and *P. innesi* have arrived at different results. For *P. axelrodi*, Post (1965: 65) found n = 24 while Scheel and Christensen (1970: 26) found n = 26. Post (1965) did not describe chromosome morphology, but Scheel and Christensen (1970: 31) state that the chromosomes include one pair with "short or very short secondary arms," with the rest "strictly one-armed" (see their figure on page 31). For *P. innesi* the latter authors (pp. 26, 31) give 2n = 32 as the chromosome number. They describe all as having "two arms," state that "twenty large two-armed elements represent derived elements produced by fusions of one-armed elements." Lueken and Foerster (1969: 172) report 2n = 36 for *P. innesi*, but our count from their Figure 3 is 2n = 32, which agrees with that of Scheel and Christensen. Scheel (1972: 62) gives the karyotype of *P. simulans* as n = 25 and 48 arms.

It is obvious that some disagreement about the karyotype of these fishes exists, and it is even more unfortunate that the above authors either presented their data without illustrations or in the form of photographs of crude cell squashes, with no presentation of serially arranged chromosomes, no indication of numbers of cells examined, no list of tissue examined, no locality data of examined specimens, and no voucher specimens deposited in museums. There is agreement among the authors that all three of the neon tetras have different karyotypes and we will present our discussion on the assumption that these differences are real.

Scheel and Christensen (1970: 31) and Scheel (1972: 65) attempted to use karyotypic data to determine whether the neon tetras are "closely related" and concluded that all are "distantly related," thereby implying that the three species should be kept in separate genera. Further, based on similarity of chromosome morphology and

number, Scheel (1972: 65) considered the following characids to be closely related: *Hasemania marginata*, *Moenkhausia oligolepis*, *Thayeria boehlkei*, *Triportheus pictus*, *Hemigrammus caudovittatus*, *Hyphessobrycon bifasciatus*, *Nematobrycon palmeri*,[1] *Astyanax bimaculatus*, and *Gymnocorymbus ternetzi*. Scheel never explicitly defined the character he used to form this group, but our interpretation of his text is that the karyotype of each member has at least one, but up to five, large metacentric chromosomes. The only way to define the character as it was used is "presence of large metacentric chromosomes," disregarding the number of metacentrics. The logic of such a procedure escapes us. Nevertheless, in effect Scheel proposed a phylogenetic hypothesis greatly at variance with any current understanding of characid relationships. In spite of his statement that the karyotype shared by this assemblage could not possibly have developed independently, implying monophyletic relationship, we would hold that many characters in the morphology of these fishes would refute such a hypothesis, especially the putative "close relationships" of *Triportheus* and *Nematobrycon* with each other and with the other genera listed above. We suspect that sister group relationships will indeed be found between some species currently assigned to *Hemigrammus*, *Hyphessobrycon*, and *Hasemania*, but the evidence as presented and analyzed by Scheel is not suitable for the analysis. Instead, the data presented by Scheel (1972) indicate to us that gross chromosome morphology as studied by the above authors is quite labile in small characid species and that considerable comparative investigation of chromosome banding, with emphasis on the search for derived characters, will be needed before chromosome data will be useful in phylogenetic analysis of these fishes.

Based on data presented by the above authors, we note that each of the neon tetras has a karyotype different from the others, that both *P. simulans* and *P. axelrodi* have karyotypes which are similar to those of many other small characid species, and that *P. innesi* seems to have a unique, probably derived, karyotype. These data thus are not relevant to phylogenetic analysis since the characters are either primitive for characids or are autapomorphic.

[1] Incorrectly placed in the Cheirodontinae.

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Genus *Stizus* Latreille in North America (Hymenoptera: Nyssoninae)

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GENUS *STIZUS* LATREILLE IN NORTH AMERICA (HYMENOPTERA: NYSSONINAE)

J. WILLIAM STUBBLEFIELD[1]

ABSTRACT. The five North American species of *Stizus* Latreille are reviewed. *Stizus aztecus* is described, and new descriptions are provided for the other four species: *S. brevipennis* Walsh, *S. texanus* Cresson, *S. occidentalis* Parker, and *S. iridis* Dow. A key to these species is provided, and the distribution of each species is documented. The North American species belong to two well-defined species-groups, the *brevipennis* group and the *ruficornis* group, and the characters defining these two groups are discussed. The ethology of *Stizus* is reviewed, and a worldwide list of the published prey records is presented.

INTRODUCTION

The species belonging to the genus *Stizus* are large, often brightly colored, ground-nesting wasps that provision their nests with Orthoptera. With more than 120 species now recognized, *Stizus* is one of the largest genera in the Nyssoninae with only the cosmopolitan genera *Bembecinus* and *Bembix* containing more species. *Stizus* is widespread in Africa, Eurasia, and North America but is absent from Australia and the Americas south of Mexico. The vast majority of species occur in the Old World, and only five species are known from North America: *S. brevipennis* Walsh, *S. texanus* Cresson, *S. aztecus* new species, *S. occidentalis* Parker, and *S. iridis* Dow. The North American species fall into two well-defined species groups, the *brevipennis* group which is restricted to North America and the *ruficornis* group which is well developed in Africa and Eurasia. Two other species groups are also recognized but do not occur in North America, the very large *fasciatus* group with numerous species in the Old World and the monotypic *scolaeformis* group of Africa.

The present work provides a review of what is now known about the North American species of *Stizus*, including their taxonomy, distribution, and ethology. A new species, *S. aztecus*, is described, and each of the previously known species is redescribed in order to remedy certain deficiencies in earlier descriptions and to facilitate comparisons between species. The male genitalia and sternum VIII of each species are illustrated with SEM photographs; these structures differ markedly between species and provide a reliable basis for identification. The characters serving to distinguish the *brevipennis* and *ruficornis* groups are discussed, and a key to the North American species is provided. It is unlikely that any new species will be discovered in North America, but much remains to be learned about the biology of *Stizus*. Prey records, for example, exist for only two of the five North American species and only eleven of the more than 100 species occurring in the Old World. Even less is known about the nesting behavior of *Stizus*; only the East Asian *S. pulcherrimus* has been studied in much detail (Tsuneki, 1965). A worldwide list of prey records for *Stizus* is provided here, and Evans (1966) may be consulted for a general review of *Stizus* ethology.

A sizeable, though rather scattered, literature devoted to *Stizus* has developed since the classical monograph of Hand-

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lirsch (1892) which treated the genus on a global scale. At that time, only two species were known from North America, *S. brevipennis* Walsh (1869) and *S. texanus* Cresson (1872), and several decades were to pass before Parker (1929) described *S. occidentalis*. Dow (1941) added *S. iridis* and provided the first comprehensive key to the North American species. The world monograph of Handlirsch (1892) provided a firm foundation for further work on *Stizus* taxonomy and is a valuable source of information even today. The more recent literature is much narrower in scope but includes several important regional works, including Mercet (1906) for Spain, Mochi (1939) for Egypt, Bingham (1897) for India, and Arnold (1929, 1945) for southern Africa and Madagascar. There is a need for a comprehensive review of the Old World *Stizus* with an eye toward developing a clearer view of subgeneric relationships. Valuable discussions of the systematics of *Stizus* and related genera have been provided by Lohrmann (1943), de Beaumont (1954), Evans (1966), and Bohart and Menke (1976). This last work includes a comprehensive list of the known species. The morphological terminology employed here follows Bohart and Menke (1976) or, in some cases, Evans (1966).

The genus *Stizus* was interpreted in a very broad sense by such early authors as Handlirsch (1892), Fox (1895), Kohl (1897), and, most recently, by Arnold (1929, 1945). As understood by these authors, *Stizus* included two components which have been generally regarded as distinct genera following Parker (1929): *Stizoides* Guérin-Méneville and *Bembecinus* A. Costa. These genera agree with *Stizus* in many respects and are generally considered to be closely related. *Stizoides* is clearly very close to *Stizus* but differs in having edentate mandibles, eyes that converge strongly below, and a strongly sculptured integument. The distribution of *Stizoides* is very similar to that of *Stizus*; the 28 species now recognized are restricted to Africa and Eurasia except for two North American species. *Bembecinus* represents a more divergent element as indicated by the following derived characters that serve to distinguish it from *Stizus* and *Stizoides*: 1) male antenna with a spinose projection on flagellomere IX in most species; 2) episternal-scrobal sulcus absent, the mesopleuron not interrupted by any grooves or ridges; 3) propodeum concave behind, compressed into ridges posterolaterally; 4) second submarginal cell markedly narrowed anteriorly and sometimes petiolate; and 5) hindwing median cell with only one distal appendage instead of two. The roughly 150 species currently recognized in *Bembecinus* include representatives in all major regions. *Stizoides* and *Bembecinus* both lack the median pubescent depression on the female scutellum as found in many *Stizus*.

The behavioral information now available strongly supports this generic classification (Evans, 1966). *Stizus* provisions with Orthoptera (and rarely, perhaps, with cicadas, see Table 1) while *Bembecinus* preys upon small Homoptera (Cicadoidea except cicadas, Fulgoroidea, and, rarely, Psylloidea). Most, if not all gorytine wasps also employ homopteran prey, and the use of such prey by *Bembecinus* may well represent the retention of the primitive prey preference. *Stizoides*, on the other hand, is a cleptoparasite of sphecids that prey upon Orthoptera, including the genera *Palmodes*, *Prionyx*, and *Sphex*. *Stizus* and *Bembecinus* further differ in that the former oviposits on the first prey item in each cell and employs mass provisioning, while the latter oviposits on a mound of soil in the empty cell and practices progressive provisioning.

Most recent authors have treated *Stizus*, *Stizoides*, and *Bembecinus* as comprising the tribe Stizini which is generally regarded as being more or less intermediate between the Gorytini and the Bembicini. There can be little doubt that the Stizini and the Bembicini are closely related since they uniquely share a number

of clearly derived characters, including: 1) forewing with basal vein reaching subcosta far basad of the pterostigma so that the prestigmal portion of the first submarginal cell is longer than the distance between the marginal cell and the apex of the wing; 2) scutellum with a lamellate posterior border that broadly overlaps the metanotum which is thus hidden laterally; and 3) male tergum VII with basolateral spiracular lobes (absent in the bembicin genera *Bicyrtes* and *Microbembex*). These characters are considered to be derived because they occur in no other sphecoid wasps including those generally considered to be most primitive. The only exception is the presence of well-developed spiracular lobes in the African genus *Handlirschia* (Bohart and Menke, 1976) now assigned to the Gorytini but perhaps more closely related to the Stizini than has been generally recognized. The Stizini are distinguished from the Bembicini by the presence of certain primitive characters in the former, notably: 1) labrum distinctly wider than long; 2) ocelli normal; and 3) midtibia with two spurs (except in some *Stizoides*). I have been unable to find any clearly derived characters that would uniquely associate the Stizini, and it is probable that this tribe should be combined with the Bembicini.

A few genera included in the Gorytini bear a more or less striking resemblance to the Stizini in that they are relatively large wasps of robust proportions with a notably compact mesosoma. In some cases, as in *Sphecius*, the resemblance extends to such features as a prominent and fully exposed labrum, very small pterostigma, and a smoothly curved episternal-scrobal sulcus. Although these are apparently derived characters in the Nyssoninae, they are known to have arisen more than once in the Sphecoidea, and their presence in some Gorytini and the Stizini may represent parallel developments rather than shared ancestry. In any event, *Sphecius* is the only gorytin genus in North America that is likely to be confused with *Stizus* but can be readily separated by the presence of a well-defined omaulus and a much shorter first submarginal cell.

I have examined material from the following collections which are here provided with abbreviations in order to facilitate subsequent reference: American Museum of Natural History (AMNH), Bee Biology and Systematics Laboratory, USDA, Logan, Utah (BBSL), Los Angeles County Museum of Natural History (LACM), Museum of Comparative Zoology (MCZ), Philadelphia Academy of Natural Science (PAS), Texas A&M University (TA&M), United States National Museum (USNM), University of California at Davis (UCD), University of California at Riverside (UCR), and my personal collection (JWS).

Genus *Stizus* Latreille

Stizus Latreille, 1802–1803, Hist. Nat. Gen. Partic. Crust. Ins. **3:** 344. Type species: "*Stizus ruficornis* Fabr." [=*Larra ruficornis* of Fabricius, 1804, = *Bembex ruficornis* Fabricius, 1787, = *Vespa ruficornis* Forster, 1771] designated by Blanchard, 1846: pl 121. Synonymy after J. van der Vecht, 1959, Ent. Ber. **19:** 68–69; this species should be referred to as *Stizus ruficornis* (Forster) rather than *Stizus ruficornis* (Fabricius) as it has usually been written. Most authors, including Pate, 1937, have accepted Latreille, 1810, as a type-designation for *Stizus*, but see Bohart and Menke, 1965, Bull. zool. Momencl. **22:** 255–256 and Bohart, 1966, Bull. zool. Nomencl. **23:** 7–8.

1803 Latreille, Hist. Nat. Gen. Partic. Crust. Ins. **5:** 309.

1805 Latreille, Hist. Nat. Gen. Partic. Crust. Ins. **13:** 302 (in part).

1809 Latreille, Genera Crust. et Ins. **4:** 100 (in part).

1810 Latreille, Considér. génér. p. 321 (in part).

1846 Blanchard, Hyménoptères, pp. 113–227 (vol. 13), pls. 107–129 (vol. 14). *In* G. Cuvier, La Regne Animal etc. Fortin, Masson et Cie, Paris.

1892 Handlirsch, Sitzber. k. Akad. Wiss. Wien, Math. -nat. Classe, Abt. 1, **101**(1): 25–205, 3 pls. (in part).

1895 Fox, Proc. Acad. Nat. Sci. Philadelphia 1895: 264–268 (in part).

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1929 Arnold, Ann. Transvaal Museum **13:** 217, 260–319 (in part).
1929 Parker, Proc. U.S. Nat. Museum **75**(5): 5, 9–10, figs. 1, 2, 29.
1937 Pate, Mem. Amer. Ent. Soc., No. 9: 62, 85–86.
1939 Mochi, Bull. Soc. Fouad 1er d'Ent. **23:** 183–237 (in part).
1942 Dow, Psyche **48:** 171–181.
1943 Lohrmann, Mitt. Münchn. Ent. Ges. **33:** 189, 203–205.
1945 Arnold, The Sphecidae of Madagascar, pp. 68–78 (in part).
1951 Krombein, *in* Muesebeck *et al.*, Hym. of Amer. North of Mexico, Synoptic Catalog, p. 993.
1954 de Beaumont, Rev. Suisse Zool. **61**(8): 295, 313.
1955 Bytinski-Salz, *in* de Beaumont and Bytinski-Salz, Bull. Res. Counc. Israel B **5:** 32–60.
1966 Evans, Comparative Ethology and Evolution of the Sand Wasps, pp. 117–118, figs. 63–68.
1971 Tsuneki, Acta. Zool. Acad. Sci. Hungaricae **17:** 202–207, figs. 57–83.
1976 Bohart and Menke, Sphecid Wasps of the World, pp. 53, 525–527.
1979 Krombein, *in* Krombein *et al.*, Catalog of Hym. in Amer. North of Mexico, vol. 2, p. 1702.

Larra Fabricius *sensu* Klug, 1845, Insecta, decas quinta, pl. 46 and unnumbered text pages, *in* vol. 2 of C. G. Ehrenberg, 1828–1845, Symbolae physicae, seu icones et descriptiones corporum novarum aut minus cognitorum, etc. 4 vol., Barolini, Reimeri (in part).

Larra Fabricius *sensu* F. Smith, 1856, Cat. Hym. British Museum **4:** 337 (in part).

Megastizus Patton, 1897, Bull. U.S. Geol. Survey Terr. **5:** 344–345. Type species: *Stizus brevipennis* Walsh, 1869, by original designation.
1887 Cresson, Synopsis, Trans. Amer. Ent. Soc. Suppl., pp. 115, 278.
1899 Ashmead, Canad. Ent. **31:** 347.

Stizolarra Saussure, 1887, Soc. Ent. Zurich **2:** 9. Type species: *Sphex vespiformis* Fabricius, 1775, designated by Pate, 1937, p. 62.

Megalostizus Schulz, 1906, Spolia Hymenopterologica p. 199. Emendation of *Megastizus* Patton, 1879.

Generic Diagnosis: Maxillary palpi with six and labial palpi with four segments; mandible with single inner subapical tooth; labrum exposed, moderately convex, approximately semicircular in outline, plainly wider than long; male antenna without a projection on flagellomere IX; inner margins of compound eyes subparallel, only slightly converging below; ocelli normal. Mesopleuron with a smoothly curved episternal-scrobal sulcus, precoxal sulcus often evident, otherwise without ridges or grooves; scutum with oblique scutal carinae; scutellum with lamellate posterior margin overlapping metanotum; scutellum in female often with a median pubescent depression; propodeum evenly rounded posterolaterally, not compressed into ridges, spiracular groove absent. Foretarsal rake present in female; midtibia with two apical spurs. Forewing with three submarginal cells, the second not petiolate; basal vein arising before cubito-anal crossvein, joining subcosta far basad of pterostigma, first submarginal cell much longer than marginal cell. Hindwing media arising far basad of cubito-anal crossvein; median cell with two distal appendices. Tergum VII of male with large lateral lobes containing spiracles; sternum VIII of male with three distal prongs.

Generic Description: This description has been prepared as a summary of the characters shared by the North American species and may not apply in all details to members of the Old World fauna.

Male. Form robust; size large to very large (16 to 33 mm), larger than both *Stizoides* and *Bembecinus.*

Head, in facial view, wider than long (greatest width versus median length from vertex to anterior margin of clypeus), narrower than thorax. Maxillary palpus with six and labial palpus with four segments; mandible with a single inner subapical tooth; labrum exposed, moderately convex, distinctly wider than long; clypeus convex, wider than long, separated from antennal sockets by more than intersocketal distance. Supraclypeal area convex with apex of convexity near subantennal line; interantennal area with a low median ridge, often carinate posteriorly; supraantennal area with a longitudinal median depression that often surrounds the median ocellus, bordered above to each side

by more or less distinct convexities. Antennae long, reaching posterior face of propodeum, only slightly enlarged distally; scape about twice as long as greatest width; antenna with thirteen segments, flagellomeres with or without linear carinate tyloids, without a projection on flagellomere IX. Compound eyes nearly reaching clypeus, little separated from base of mandible, inner margins subparallel, only slightly converging below. Ocelli unmodified; bulge present between median ocellus and each lateral ocellus raising anterior margin of each lateral ocellus above its posterior margin.

Mesosoma robust, with sclerites smoothly confluent; pronotum short; notauli usually not evident, occasionally indicated by faint impressions; parapsidal lines and well-separated admedian lines usually present but often poorly developed and sometimes not evident; mesonotal laminae broad, each marked posteriorly by oblique scutal carina delimiting a concave declivity; metanotum hidden laterally by scutellum but in fact continuous to metapleura, with a reflexed lamelliform process along posterior margin of wing insertion; propodeum rounded posterolaterally, flattened behind; mesopleuron with well-defined episternal-scrobal sulcus forming a smoothly curved arc; omaulus, acetabular carina, and sternaulus absent. Legs without pecten on foretarsi; midtibia with two apical spurs; arolia prominent, extending to or somewhat beyond basal half of claws, subequal on all legs. Forewing with pterostigma small, not as wide as costal cell; basal vein arising basad of cubito-anal crossvein and reaching subcosta far basad of the pterostigma; first submarginal cell about twice as long as marginal cell; second submarginal cell narrower anteriorly but not petiolate, receiving both recurrent veins. Hindwing with media diverging far basad of cubito-anal crossvein, median cell with two distal appendices.

Gaster robust, with seven visible terga; tergum VII with large spiracular lobes; tergum VIII simple, without lateral lobes, hidden beneath tergum VII; sternum I with a prominent longitudinal carina basally; sternum VII exposed, centrally sclerotized with a membranous border; sternum VIII stout, with three strong distal prongs; genitalia with digitus much exceeding cuspis.

Puncturation similar in all North American species; distinctly punctate under low magnification, upper frons and mesosoma (especially propodeum) rather coarsely so; labrum, clypeus, supraclypeal area, occiput, pronotum, and gaster very finely punctate.

Vestiture consisting of scattered to rather dense long hairs; appressed pubescence also present over much of body in some species and in others restricted to legs, tegulae, sclerites at base of wing, and larger veins.

Coloration variable, ranging from mostly black with yellow markings, as in *S. brevipennis*, to mostly yellow with ferruginous and black markings, as in *S. iridis*; the other North American species exhibit various combinations of black, ferruginous, and yellow.

Female. Similar to male; antenna with twelve segments; scutellum often with a median pubescent depression (poorly developed or absent in members of the *brevipennis* group); foretarsal rake well developed, forebasitarsus with six stout apical bristles; gaster with six visible terga, with or without a well-defined pygidial area on tergum VI.

Larva. Evans (1964, pp. 255–257, pl. 11, figs. 26–30) has described the larva of *Stizus pulcherrimus* (Smith) from portions of a cast larval skin extracted from a cocoon. Apparently, no other information is available on the larval morphology of *Stizus*. According to Evans, the larva may be briefly characterized as follows: Sides of apical margin of labrum with only some weak, barely protruding bristles; oral surface of prementum papillose; spinules in median portion of epipharynx directed basad, the sides of the epipharynx par-

TABLE 1. PREY RECORDS FOR SPECIES OF *Stizus*.

Species and notes	Prey	Source
1. *atrox* Smith (=*pentheres* Handlirsch) South Africa	Orthoptera nymphs	Brauns, 1911
2. *berlandi* Arnold Madagascar; unspecified number of females taken with prey	Acrididae ? "various species of grasshoppers"	Arnold, 1945
3. *brevipennis* Walsh Kansas; single female observed hunting	Tettigoniidae *Conocephalus* sp. (=*Xiphidium* sp.)	Williams, 1914
4. *chrysorrheous* Handlirsch South Africa	Orthoptera nymphs	Brauns, 1911
5. *dewitzii* Handlirsch South Africa	Orthoptera nymphs	Brauns, 1911
6. *fasciatus* (Fabricius) Corsica	Acrididae Acridinae *Chorthippus bicolor* Charp. Calliptaminae *Calliptamus italicus* Linn. Cyrtacanthacridinae *Pezotettix giornae* Rossi	Ferton 1899, 1902a,b 1909
fasciatus (Fabricius) Spain	Acrididae Acridinae *Stauroderus vagans* Eversman	Bernard, 1934
fasciatus (Fabricius) Israel; aggregation of more than 100 nests with females carrying stated prey	Acrididae Calliptaminae *Calliptamus* sp.	Bytinski-Salz, 1955
7. *fuscatus* Morice Libya; single female taken with prey	Acrididae "3d instar desert locust"; presumably *Schistocerca gregaria* Forskål (Cyrtacantharidinae)	de Beaumont, 1956
8. *imperialis* Handlirsch South Africa	Acrididae (mostly)	Brauns, 1911
9. *iridis* Dow Utah; two nests excavated	Acrididae Oedipodinae *Trimerotropis pallidipennis* (Burmeister) *Trimerotropis sparsa* (Thomas)	Dow, 1976
10. *marshalli* Turner Zimbabwe (Southern Rhodesia)	Mantidae	Dow, 1935
11. *pulcherrimus* (Smith) Japan	Acrididae Acridinae *Aiolopus tamulus* Fab.	Katayama, 1933
pulcherrimus (Smith) East Mongolia; single nest studied	Acrididae Acridinae *Chorthippus dubius* Zub.	Tsuneki, 1943a, 1965
pulcherrimus (Smith) Korea; 15 nests excavated containing 118 prey items, the most detailed behavioral study yet to appear	Acrididae Acridinae *Acrida lata* Motschulsky *Aiolopus tamulus* Fab. *Parapleurus alliaceus* Germar *Stauroderus schmidti* Ikonnikov	Tsuneki, 1943b, 1965

TABLE 1. CONTINUED.

Species and notes	Prey	Source
	Oedipodinae *Trilophidia annulata* Thunberg Cyrtacanthacridinae Sp. near *Oxya vicina* Brunner Tettigoniidae Conocephalinae *Conocephalus maculatus* Zub.	
12. *rufescens* (Smith) India; single female observed with prey, a questionable record	"small cicada"	Bingham, 1897
13. *ruficornis* (Forster) (=*ruficornis* Fabricius) France	Mantidae *Mantis religiosa* Linn. and other mantids	Fabre, 1886
ruficornis (Forster) (=*distinguendus* Handl.) La Camargue, France; several nests studied	Mantidae *Mantis religiosa* Linn. *Empusa egena*	Deleurance, 1941

tially pigmented; mandibles tridentate, middle tooth very large, blunt, and close to the apical tooth; body with restricted transverse rows of large, darkly pigmented spines. Evans further notes that the arrangement of the median epipharyngeal spinules and the presence of a stout preapical tooth on the mandible set *Stizus* apart from all other nyssonines and are suggestive of similar structures in the Sphecinae. He suggests that this unexpected resemblance may be associated with the use of orthopteran prey in both *Stizus* and many sphecines.

Distribution: Stizus is widely distributed in the Ethiopian, Palearctic, and Nearctic Regions but is apparently absent from the New World south of central Mexico, Southeast Asia, Australia, and the islands of Oceania. Of the more than 120 species currently recognized in *Stizus*, only five are known from North America where they are largely restricted to arid or semiarid regions, the principal exception being *S. brevipennis* which is widely distributed in the Austral Zone east of the Rocky Mountains. The other North American species are restricted to the western half of the continent.

Behavior: Behavioral information on *Stizus* is very limited. Only the East Asian *S. pulcherrimus* (Smith) has been studied in some detail (Tsuneki, 1943a,b, 1965). Dow (1976) has provided the only report on the nesting behavior of a North American species. Evans (1966) has thoroughly reviewed the behavioral literature on *Stizus*. To judge from existing accounts, the nesting behavior of *Stizus* may be briefly summarized as follows. The nests are constructed in the ground and consist of a main burrow ending in one or more brood cells. Often a number of females will nest in close proximity and such nesting aggregations are sometimes quite large; Bytinski-Salz (1955) has reported an aggregation of more than 100 nests of *S. fasciatus* in Israel. The nest entrance is closed when the wasp is away, and false burrows, which are thought to deter parasites, are sometimes constructed near the true nest entrance (Tsuneki, 1965). The egg is laid on the first prey item before the rest of the prey are brought in, and the larva may reach a considerable size before provisioning is completed (Tsuneki, 1965). Such provisioning behavior may be viewed as transitional between mass provisioning and true progressive provisioning. Miltogrammine sarcophagids, rhipiphorid beetles,

and mutillid wasps are reported parasites (Evans, 1966). In all certain cases, *Stizus* has been found to use orthopteran prey; grasshoppers, katydids, and mantids have all been reported. Bingham (1897: 277) reported, however, that he observed a female of *S. rufescens* (Smith) with a small cicada, but, in view of the other evidence, this record must be considered doubtful and in need of confirmation. One might suppose that Bingham actually saw a member of the superficially similar genus *Sphecius* which is well known to hunt cicadas, but Bohart and Menke (1976) do not list any *Sphecius* from India where Bingham made his observation. Table 1 lists all the prey records for *Stizus* that have come to my attention and can serve as a guide to the literature on the biology of *Stizus*.

Species Groups: Four species groups are currently recognized in *Stizus*, the *fasciatus*, *ruficornis*, *brevipennis*, and *scolaeformis* groups. The first three date from the world monograph of Handlirsch (1892) which treated *Stizus* in a very broad sense including two segregates now considered to have generic status, *Stizoides* Guérin-Méneville (corresponding to the *tridentatus* group) and *Bembecinus* A. Costa (including the nine other species groups recognized by Handlirsch). The monotypic *scolaeformis* group was erected by Arnold (1929) for the peculiar African species of that name. The *fasciatus* group is restricted to Africa and Eurasia; the *ruficornis* group also occurs in Africa and Eurasia but includes two North American species, and the *brevipennis* group occurs only in North America.

The *fasciatus* group is by far the largest and includes more than two thirds of the known species. Most of the remaining species belong to the *ruficornis* group, which takes its name from the type species of the genus. The principal difference between these groups is the presence of a well-defined, median, pubescent depression on the female scutellum in the *ruficornis* group but not the *fasciatus* group. Handlirsch (1892) also noted that the first intercubital vein is straight in the *ruficornis* group but somewhat curved with the convexity toward the apex of the wing in the *fasciatus* group. This venational difference, however, is slight at best, and its value as a distinguishing character has been questioned by Arnold (1929) and Lohrmann (1943), who noted that males cannot be reliably assigned to one group or the other in the absence of the associated females. The close similarity between the *fasciatus* and *ruficornis* groups has been noted by several authors, and Lohrmann (1943) pointed out that a weakly developed scutellar pit is present in several species generally assigned to the *fasciatus* group. He considered it likely that the *ruficornis* group is a polyphyletic derivative of the *fasciatus* group. These two groups taken together include more than 95% of the species currently recognized in *Stizus*, and it is to be hoped that a more solid basis for subdividing this large complex will eventually be discovered.

The other two species groups are clearly distinct but include very few species. Handlirsch (1892) recognized the *brevipennis* group on the basis of distinctive features of the male gaster. The relatively narrow sternum VIII with strongly downcurved prongs and the pointed apical projections on the digitus are apparently unique to this group. Handlirsch (1892) and Lohrmann (1943) considered the *brevipennis* group to be closely allied to the *fasciatus* group, but this conclusion is based on the fact that both groups retain certain primitive characters that provide little evidence for a close relationship. The principal similarities are: 1) female scutellar pit absent or at most only weakly developed in both groups, and 2) a well-defined pygidial plate bordered by carinae present in the *brevipennis* group and some members of the *fasciatus* group. As noted below, the *fasciatus* group shares several derived characters with the *ruficornis* group, and there would seem to be little doubt that these groups are more

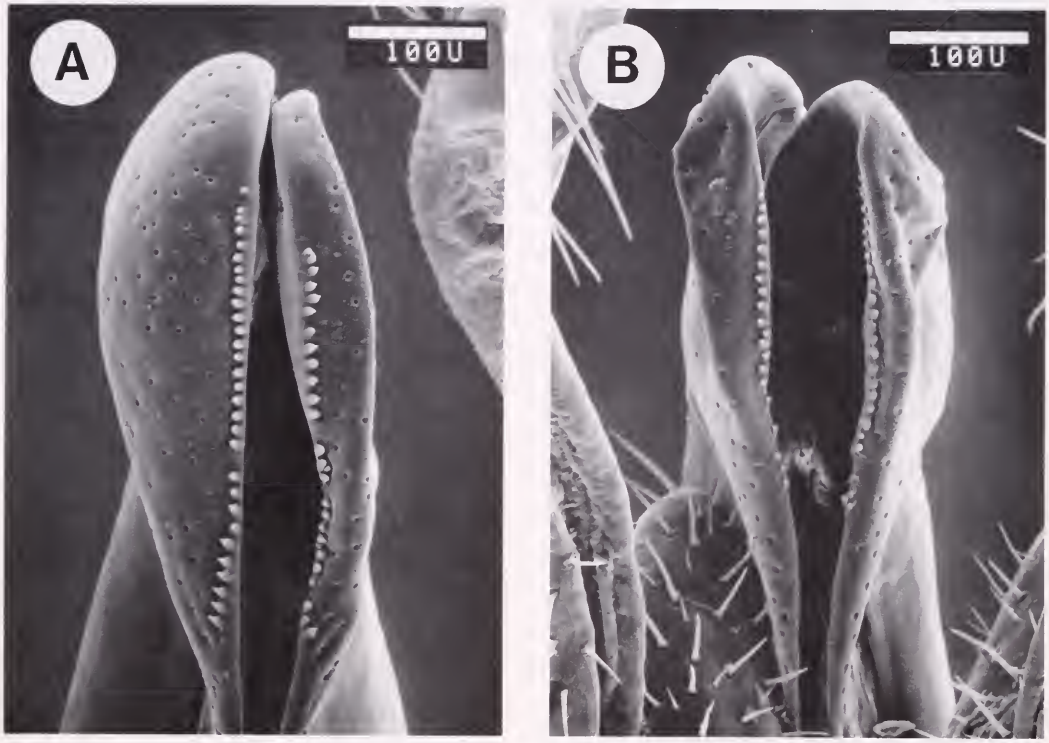

Figure 1. Apical enlargement of aedeagus in ventral view showing rows of minute teeth. A. *Stizus iridis* Dow. B. *Stizus occidentalis* Parker.

closely related to each other than either one is to the *brevipennis* group. The *scolaeformis* group includes only a single unusual species that could be viewed as representing a separate subgenus as noted by Arnold (1929). This species possesses a female scutellar pit as in the *ruficornis* group, a well-marked female pygidial plate as in the *brevipennis* group and some members of the *fasciatus* group, a carina to each side of the median carina on sternum I as in some *Stizoides*, and differs from all other species in having a much lengthened pronotum with an oblique anterior face instead of a shorter pronotum forming a discoid collar.

The North American *Stizus* represent two well-defined groups, the strictly Nearctic *brevipennis* group including *S. brevipennis*, *S. texanus*, and *S. aztecus* and the mostly Old World *ruficornis* group including *S. occidentalis* and *S. iridis*. Selected characters serving to distinguish the two groups are listed in Table 2. Several of the cited characters have not been noted by previous authors, and their distribution in the Old World species remains to be determined. It should be noted, however, that some of the characters cited for the North American species of the *ruficornis* group also occur in at least some members of the Old World *fasciatus* group. Flagellar tyloids, a broad and flat sternum VIII, and an evenly rounded digitus, for example, occur in both groups (see figs. in Mochi, 1939). Similarly, my dissections have revealed the presence of a carina on the inner surface of sternum VII in males of *S. imperialis*, *S. marthae* (=*cheops*), and *S. vespiformis* of the *fasciatus* group as well as *S. combustus* (=*fuliginosus*), and *S. ruficornis* of the *rufi-*

TABLE 2. SPECIES GROUP CHARACTERS IN NORTH AMERICAN *Stizus*.

brevipennis group	*ruficornis* group (North American species)
1. Head in facial view with vertex convex, lateral ocelli not projecting above vertex.	1. Head in facial view with vertex nearly straight, lateral ocelli projecting above vertex.
2. Male antenna without tyloids.	2. Male antenna with tyloids on some flagellomeres.
3. Female scutellum with median pubescent depression poorly developed or absent.	3. Female scutellum with well-defined median pubescent depression.
4. Lower posterior face of propodeum with a pair of carinae extending upward from the submarginal sulcus.	4. Lower posterior face of propodeum without a pair of carinae.
5. Female tergum VI with a well-defined pygidial plate bordered by carinae.	5. Female tergum VI without a pygidial plate.
6. Male sternum VII without a carina on inner surface.	6. Male sternum VII with a longitudinal carina on inner surface.
7. Male sternum VIII narrow with lateral prongs strongly downcurved.	7. Male sternum VIII broad with lateral prongs nearly straight.
8. Male genitalia with digitus produced into pointed projections distally.	8. Male genitalia with digitus evenly rounded distally.
9. Apical portion of aedeagus without minute teeth.	9. Apical portion of genitalia with minute teeth on ventral margin as shown in Figure 1.
10. Appressed pubescence generally distributed over body.	10. Appressed pubescence restricted to legs, larger veins, and sclerites base of wings.

cornis group. These shared characters further emphasize the similarity of the *fasciatus* and *ruficornis* groups and reveal the distinctive nature of the *brevipennis* group. Indeed, there would seem to be sufficient grounds for treating the *brevipennis* group as a separate subgenus for which the name *Megastizus* Patton is available, but I hesitate to do so without examining more Old World material.

In any event, the North American *Stizus* represent two distinct lineages that may well date from early in the diversification of the genus. The *ruficornis* group would seem to be more advanced as evidenced by such apparently derived characters as flagellar tyloids, well-marked female scutellar pit, absence of a pygidial plate, longitudinal carina on male sternum VII, and minute teeth on the aedeagus. Most of these are also present in the *fasciatus* group, and it may well be that the *brevipennis* group represents the most generalized living *Stizus*, although the Old World fauna must be examined more thoroughly before this can be said with confidence. It is very likely that the North American species of the *ruficornis* group represent a relatively recent invasion from Eurasia, presumably by way of the Beringian connection. The *brevipennis* group, on the other hand, has probably been in North America for a much longer time and may date from before the separation of North America and Europe during the Eocene. Unfortunately, no fossil *Stizus* have yet been discovered.

KEY TO THE NORTH AMERICAN SPECIES OF *STIZUS*

1. Males; antenna with 11 flagellomeres; gaster with 7 visible terga 2
   Females; antenna with 10 flagellomeres; gaster with 6 visible terga 6
2. Flagellomeres without tyloids; sternum VII without carina on inner surface; sternum VIII (Figs. 2, 3 and 4) relatively narrow with lateral prongs strongly downcurved. (*brevipennis* group) 3
   Flagellomeres VII and VIII with linear carinate tyloids; sternum VII with a median

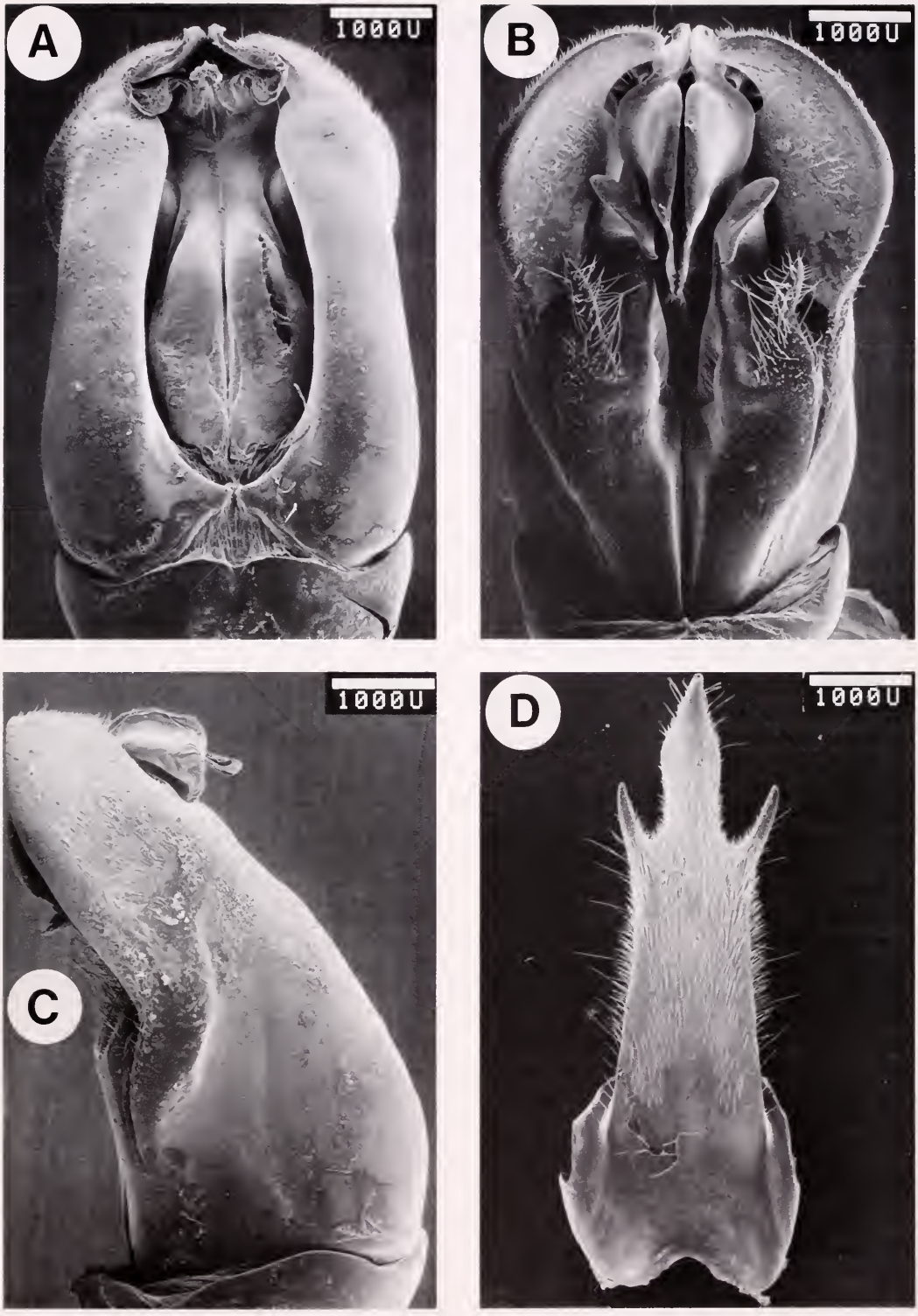

Figure 2. *Stizus brevipennis* Walsh. Male genitalia in A. dorsal, B. ventral, and C. lateral views; D. male sternum VIII, ventral view.

longitudinal carina on inner surface; sternum VIII (Figs. 5 and 6) relatively broad with lateral prongs nearly straight. (*ruficornis* group) 5

3. Anterior margin of clypeus tri-emarginate, the median emargination very shallow; tergum VII broadly rounded posteriorly, without a median emargination; sternum VI deeply emarginate apically; sternum VII with heavily sclerotized portion narrowly triangular, tapering to a point apically; sternum VIII with median prong subparallel basally (Fig. 2) ..... *brevipennis* Walsh

   Anterior margin of clypeus evenly rounded; tergum VII abruptly narrowed and flattened posteriorly with a small median emargination; sternum VI shallowly emarginate apically; sternum VII with heavily sclerotized portion truncate and shallowly emarginate apically; sternum VIII with median prong broadly triangular, not subparallel basally 5

4. Genitalia (Fig. 3) relatively slender with longitudinal axis almost perpendicular to basal margin in lateral view; apical enlargement of aedeagus narrower than distance from tip to tip of the two pointed projections at the apex of each digitus ..... *texanus* Cresson

   Genitalia (Fig. 4) more robust with longitudinal axis oblique to basal margin in lateral view; apical enlargement of aedeagus wider than distance from tip to tip of the two pointed projections at the apex of each digitus ..... *aztecus* new species

5. Distinct tyloids present on flagellomeres V to IX; posterior margin of clypeus nearly straight; sides of first tergum slightly convex in dorsal view; mesopleura, metapleura, and propodeum mostly or entirely black ..... *occidentalis* Parker

   Distinct tyloids present on flagellomeres IV to XI; posterior margin of clypeus slightly but distinctly emarginate; sides of first tergum concave in dorsal view; mesopleura (except ventrally), metapleura, and propodeum almost entirely yellow ..... *iridis* Dow

6. Head in facial view with vertex convex, lateral ocelli not projecting above vertex; tergum VI with a well-defined pygidial plate bordered by carinae; appressed pubescence widely distributed (*brevipennis* group) 7

   Head in facial view with vertex nearly straight, lateral ocelli projecting above vertex; tergum VI without a well-defined pygidial plate; appressed pubescence restricted to legs, larger veins, and axillary sclerites (*ruficornis* group) 9

7. Anterior margin of clypeus with a broad, medially angulate emargination; lower margins of tergum VI strongly sinuous in lateral view ..... *brevipennis* Walsh

   Anterior margin of clypeus with a shallow, rounded emargination; lower margins of tergum VI with basal three quarters nearly straight in lateral view 8

8. Scutellum and metanotum marked with yellow, often extensively so ..... *texanus* Cresson

   Scutellum and metanotum entirely ferruginous without yellow maculations ..... *aztecus* new species

9. Posterior margin of clypeus nearly straight; sides of tergum I slightly convex in dorsal view; mesopleura, metapleura, and propodeum mostly or entirely black ..... *occidentalis* Parker

   Posterior margin of clypeus shallowly emarginate; sides of tergum I concave in dorsal view; mesopleura (except ventrally), metapleura, and propodeum almost entirely yellow ..... *iridis* Dow

Stizus brevipennis Walsh

1869 *Stizus brevipennis* Walsh, Amer. Entomologist **1**(8): 162. ♂.
1875 *Larra brendeli* Taschenberg, Zeitschr. f. d. Ges. Naturwiss. **45:** 361. ♂.
1879 *Megastizus brevipennis* (Walsh). Patton, Bull. U.S. Geol. Terr. **5:** 345. ♂♀.
1880 *Megastizus brevipennis* (Walsh). Taschenberg, Zeitschr. f. d. Ges. Naturwiss. **53:** 779.
1887 *Megastizus brevipennis* (Walsh). Cresson, Synopsis, Trans. Amer. Ent. Soc., Supp., p. 278 (in part).
1892 *Stizus brevipennis* Walsh. Handlirsch, Sitzber. k. Akad. Wiss. Wien, Math.-nat. Cl., Abt. 1, **101**(1): 174, pl. 1, fig. 13, pl. 2, fig. 28, pl. 3, fig. 15. ♂♀.
1895 *Stizus brevipennis* Walsh. Fox, Proc. Acad. Nat. Sci. Philadelphia 1895: 266–268. ♂♀.
1908 *Stizus* (*Megastizus*) *brevipennis* Walsh. Johnson and Rohwer, Ent. News **19**(8): 374.
1917 *Stizus brevipennis* Walsh. Mickel, Univ. Nebraska Studies **17**(4): 117.
1941 *Megastizus brevipennis* (Walsh). Snodgrass, Smiths. Misc. Coll. **99**(14): pl. 19, figs. A–G. Male genitalia.
1942 *Stizus brevipennis* Walsh. Dow, Psyche **48:** 176–178, 180–181 (key), fig. 6.
1965 *Stizus brevipennis* Walsh. Chandler, Proc. Indiana Acad. Sci. **75:** 142.
1966 *Stizus brevipennis* Walsh. Evans, Comp. Ethol. Evol. Sand Wasps, p. 117, figs. 63–68.
1976 *Stizus brevipennis* Walsh. Bohart and Menke, Sphecid Wasps of the World, pp. 524–526, fig. 180K.

Male: Length 26 to 31 mm.

Structure. Head in facial view with lateral ocelli not projecting above the rounded vertex. Clypeus with apical margin tri-

emarginate, the median emargination very shallow; supraclypeal area relatively long, width/length about 2.34 (width measured between compound eyes at lower margin of antennal sockets, length measured along midline from posterior margin of clypeus to lower margin of antennal sockets); median frontal depression surrounding midocellus. Flagellum without tyloids; apical flagellomere distinctly emarginate within. Mandible with a prominent subapical tooth set off by a distinct notch, closer to apex than in *S. texanus*; ridge extending basad along inner surface from subapical tooth distinctly convex in anterior view of spread mandibles.

Mesosoma in dorsal view similar to *S. texanus*, not as robust as in *S. aztecus*; width across pronotal lobes 5 to 7 mm, typically about 6.5 mm; scutum with notauli present as indistinct, faint impressions; admedian lines present as simple impressed lines; parapsidal lines present, not carinate and not extending to the posterior margin; scutal laminae with posterior margin behind oblique scutal carina produced into a distinct lobe; lower posterior face of propodeum with a pair of carinae extending upward from submarginal sulcus. Length of forewing 15.5 to 19.5 mm, typically about 17.5 mm.

Gaster robust; tergum VII narrowed posteriorly, apex evenly rounded; spiracular lobes broad, about twice as long as wide, broadly triangular at apex. Sternum VI deeply emarginate apically; sternum VII with heavily sclerotized portion narrowly triangular, tapering to a point, without carina on inner surface; sternum VIII as shown in Figure 2, narrow, median prong arched downward with sides subparallel basally. Genitalia as shown in Figure 2, cupsides hairy.

Vestiture. Short appressed pubescence generally distributed over body; suberect pale hairs also present, densest and most conspicuous on upper clypeus, lateral margins of frons, vertex, occiput, mesosoma generally (longer on propodeum and lower lateral and ventral portions of mesopleura), and anterior face of tergum I, sparse on genae, pronotum, and sterna, virtually absent from terga. Wings densely clothed with erect setae, gradually replaced with short appressed pubescence basally and toward anterior margin; larger veins with short appressed pubescence.

Color. Black marked with pale yellow and ferruginous.

Head mostly black, sometimes partly replaced with ferruginous especially on the vertex and occiput in specimens from more western localities; labrum and clypeus pale yellow bordered apically with a narrow band of ferruginous; supra-clypeal area and inner orbits to level of anterior ocellus pale yellow except for a black line along posterior margin of clypeus, dark extensions upward from tentorial pits sometimes present; narrow postorbital stripe pale yellow. Palpi and galeae pale yellowish ferruginous; mandible dark apically and basally, shading to yellow on outer surface. Scape yellow below and black shading to ferruginous above; pedicel and basal half of flagellomere I ferruginous, darker above and paler or even yellowish below; flagellomere II sometimes ferruginous basally on lower surface; apical flagellomere orange apically and on ventral surface; penultimate flagellomere sometimes orange except basally; the remainder of flagellum fuscous, sometimes shading to a hint of ferruginous ventrally at apex of some flagellomeres, sometimes more extensively ferruginous in western specimens.

Mesosoma mostly black, sometimes more or less extensively replaced with ferruginous in western specimens especially on pronotum, mesopleura above, scutellum, and propodeum; pronotum with pale yellow dorsal margin which is often wider to each side and sometimes shades to ferruginous anteriorly; distal half of pronotal lobes pale yellow; scutum laterally, tegulae, and base of wings ferruginous, sometimes tending to yellow; scutal disk usually black but sometimes partly replaced with ferruginous in western specimens;

scutellum with or without lateral pale yellow spots; metanotum with a yellow band. Wings subhyaline, lightly suffused with amber which tends to be darker along the second recurrent vein; veins of both wings ferruginous except for the costal vein of the forewing and the veins surrounding the marginal cell which tend to be darker, almost brown. Legs mostly yellow, more or less suffused with ferruginous; coxae, trochanters, and femora basally black, sometimes largely replaced with ferruginous in western specimens; femora ferruginous with ventral surface more or less yellow.

Gaster mostly black, sometimes partly replaced with ferruginous in western specimens, especially on terga I and II; first four terga with pale yellow lateral spots, those on terga I and II widely separated medially and rounded, subquadrate, or slightly oblong, those on terga III and IV only narrowly separated medially or continuous, much elongate. Sterna mostly black, sometimes partly replaced with ferruginous especially in western specimens; sternum II sometimes with a pair of small, widely separated, pale yellow spots; sterna III and IV with a pair of subtriangular, pale yellow, lateral spots of variable size; sternum VIII straw-colored. Genitalia ferruginous.

Female: Similar to male; length 22 to 33 mm.

Structure. As in male, aside from the usual sexual differences and the following exceptions: clypeus with a shallowly V-shaped emargination apically; apical flagellomere curved but not distinctly emarginate within; parapsidal lines sometimes extending to posterior margin of scutum. Width across pronotal lobes 6 to 7 mm. Forewing length 17 to 20 mm. Apical tergum with a well defined pygidial plate bordered by carinae; lower margin of tergum VI strongly sinuous in lateral view (see Dow, 1941: fig. 6).

Vestiture. As in male.

Color. Similar to male, exhibiting a similar range of variation.

Type. Walsh (1869) gave no indication of the location of the type specimen, and we are left to assume that it remained in his personal collection. Walsh died shortly after describing *Stizus brevipennis* and there is a short notice in the *American Entomologist* (1870, **2**(9): 275) to the effect that his collection was posthumously sold to the State of Illinois and that it was "temporarily deposited" in the museum of the Chicago Academy of Sciences. A historical sketch of the Academy published in 1877 cites the Walsh Collection of Insects as one of a number of collections destroyed by the Chicago fire of October 9, 1871. Dr. Henry S. Dybas (personal communication) has not been able to locate any *Stizus* in the holdings of the Field Museum of Natural History, the probable location of any existing remnants of the original Chicago Academy collections. It can be safely assumed that the type of *Stizus brevipennis* no longer exists.

Type Locality: "One taken in summer on wild parsnip flowers near Rock Island, Ill." (Walsh, 1869: 162).

Distribution: *Stizus brevipennis* is widely distributed in the eastern United States. In addition to the records cited below, this species is known to occur in North Carolina (Brimley, 1938) and Indiana (Chandler, 1954). Collection dates range from June 12 to September 3. Published floral records include only Walsh's (1869) report that the holotype was taken at flowers of "wild parsnip" and the report of Evans (1966: 125) that he has taken *S. brevipennis* at flowers of *Melilotus* and *Euphorbia* in Kansas. Records taken from specimen labels add only the genera *Ampelopsis* and *Cicuta*.

I have examined the following specimens, 42 males and 30 females:

COLORADO: *Jefferson Co.*: Golden, Chimney Gulch, ♀, (Oslar, UCD).

FLORIDA: *Alachua Co.*: Gainesville, ♂, VII-7-1918 (P. W. Fattig, USNM); ♂, VII-16-1918 (P. W. Fattig, USNM); ♂, VII-18-1918 (P. W. Fattig, USNM); 2 ♂, VII-22-1918 (P. W. Fattig, AMNH, JWS). *Co. unknown*: Cape Barrancas, ♀, (C. W. Willard, MCZ).

ILLINOIS: 2 ♂ (AMNH).

IOWA: *Henry Co.*: Mt. Pleasant, ♀, VII-?-1920 (USNM). *Woodbury Co.*: Sioux City, ♀, IX-3-1921 (A. W. Lindsay, MCZ).

KANSAS: *Butler Co.*: 1286 ft, ♀, ?-?-1916 (R. H. Beamer, USNM). *Decatur Co.*: ♂, ♀, VII-6-1925 (R. H. Beamer, USNM); ♂, VII-6-1925 (H. J. Grady, USNM). *Dickinson Co.*: 4 ♂, 2 ♀, and a copulating pair, VIII-?-1901 (J. C. Bridwell, USNM). *Douglas Co.*: Baldwin, ♂, VII-?-? (J. C. Bridwell, USNM). 900 ft, ♂ (F. H. Snow, USNM). *Greenwood Co.*: ♂, VIII-1-1923 (Beamer and Lawson, USNM). *Jewell Co.*: Montrose, ♂, VIII-11-1961 (F. P. Rindge, AMNH). *Osborne Co.*: 1557 ft, ♂, ♀, VIII-3-1912 (F. X. Williams, USNM). *Pottawatomie Co.*: Blackjack Creek, ♂, VII-2-1953 (Evans, Lin, and Yoshimoto, MCZ). *Riley Co.*: ♂, VII-20-1953 (Evans, Lin, and Yoshimoto, MCZ). Deep Creek, ♂ (USNM). Popenoe, ♀, VII-9-? (USNM); ♂, VII-3-? (USNM). *Stafford Co.*: Salt Flats Area, ♂, VIII-20-1953 (Evans, Lin, and Yoshimoto, MCZ). *Sumner Co.*: 1189 ft, ♀, ?-?-1916 (R. H. Beamer, USNM). Wellington, ♀ (H. R. Watts, USNM).

LOUISIANA: *St. Tammany Parish*: Covington, ♀, VI-12-1951 (Price, Beamers, and Wood, USNM).

MARYLAND: *Charles Co.*: Indian Head, ♂, ♀, VIII-23-1902 (Bridwell, USNM).

MISSISSIPPI: *Forrest Co.*: Hattiesburg, ♀, VII-29-1944 (C. D. Michener, AMNH).

MISSOURI: *St. Louis Co.*: St. Louis, ♀, VII-?-1911 (Coll. of P. Rau, USNM).

NEBRASKA: *Furnas Co.*: 2 ♂, 3 ♀ (PANS). Cambridge, ♀, VII-26-1921 (A.P.M., MCZ); ♂, VIII-2-1921 (A.P.M., MCZ); ♂, VIII-22-1923 (A.P.M., MCZ).

OKLAHOMA: *Carter Co.*: Ardmore, ♂, VII-11-? (C. R. Jones, USNM); ♀, VIII-18-1905 (C. R. Jones, USNM). *Marshall Co.*: Lake Texoma, 2 mi E of Willis, ♂, 4 ♀, VII-?-1965 (R. M. Bohart, UCD); ♀, VII-?-1965 (R. M. Bohart, JWS).

SOUTH DAKOTA: *Bon Homme Co.*: Springfield, ♂, VIII-27-1926 (H. C. Severin, MCZ).

TEXAS: *Bexar Co.*: ♂, VII-11-1931 (H. B. Parks, TA&M); ♂, VII-24-1932 (H. B. Parks, TA&M). San Antonio, ♂ (H. B. Parks, USNM). *Brazos Co.*: College Station, ♂, VI-12-1932 (S. W. Bromley, USNM); ♂, VI-25-1937, on flowers of *Ampelopsis arborea* (Strandtmann, MCZ). *Gonzales Co.*: Palmetto State Park, ♂, VI-20-1956 (H. E. Evans and E. G. Matthews, MCZ). *Lee Co.*: Giddings, ♀, VII-6-1948 (H. E. Evans, MCZ). *Titus Co.*: Mt. Pleasant, ♂, VI-13-1948, on flowers of *Cicuta maculata* L. (H. E. Evans, MCZ). *Washington Co.*: Washington State Park, ♀, VI-17-1956 (H. E. Evans and E. G. Matthews, MCZ). *Co. unknown*: ♂ (PANS); ♂, ♀ (Belfrage, USNM).

WISCONSIN: *Milwaukee Co.*: Milwaukee, ♂, VIII-17-1917 (S. Graenicher, MCZ).

Remarks: Stizus brevipennis is a very distinctive species easily recognized in either sex by the characters cited in the key. It is the only *Stizus* likely to be encountered east of the Mississippi River. Williams (1914) observed a female of this species hunting a short-winged adult female of *Conocephalus* in Kansas.

Stizus texanus Cresson

1872 *Stizus texanus* Cresson, Trans. Amer. Ent. Soc. **4:** 222. ♂ ♀.

1879 *Megastizus texanus* (Cresson). Patton, Bull. U.S. Geol. Surv. Terr. **5:** 345. ♂ ♀.

1878 *Megastizus brevipennis* (Walsh). Cresson, Synopsis, Trans. Amer. Ent. Soc., Supp., p. 278 (in part).

1892 *Stizus texanus* Cresson. Handlirsch, Sitz. k. Akad. Wiss. Wien, Math.-nat. Cl., Abt. 1, **101**(1): 176, pl. 1, figs. 2, 6, 14, 15; pl. 2, fig. 29; pl. 3, fig. 16.

1895 *Stizus texanus* Cresson. Fox, Proc. Acad. Nat. Sci., Philadelphia 1895: 267–268.

1897 *Stizus texanus* Cresson. Kohl, Ann. k. k. Naturhist. Hofmus., Wien 11: pl. VIII, fig. 126; pl. IX, fig. 150; pl. X, fig. 168.

1942 *Stizus texanus* Cresson. Dow, Psyche **48:** 178–179, 180 (key).

Male: Length 24 to 33 mm.

Structure. Head in facial view with lateral ocelli not projecting above the rounded vertex; clypeus with apical margin nearly straight along median half; supraclypeal area intermediate, width/length about 2.46 (measured as in *S. brevipennis*); median frontal depression surrounding median ocellus. Flagellum without tyloids, apical flagellomere distinctly emarginate within, apex more rounded than in *S. aztecus*. Mandible with a prominent subapical tooth set off by a distinct notch, further from apex than in *S. brevipennis*, ridge extending basad along inner surface from subapical tooth nearly straight in anterior view of spread mandibles.

Mesosoma robust; width across pronotal lobes 5 to 7.5 mm, typically about 6.5 mm; scutum without evident notauli; admedian lines carinate anteriorly, impressed lines posteriorly; parapsidal lines faint, not reaching posterior margin of scutum; scutal laminae behind oblique scutal carina produced into a distinct lobe. Length of forewing 19 to 22.5 mm.

Gaster robust but more slender than in *S. aztecus*; tergum VII abruptly narrowed into a flattened truncate projection with a small but distinct median emargination. Sternum VI shallowly emarginate apically; sternum VII with heavily sclerotized portion triangular, shallowly emarginate apically; sternum VIII as shown in Figure 3, mostly hidden by sternum VII, median prong broadly triangular in ventral view, not subparallel basally, prongs distinctly curved downward but not so strongly as in *S. aztecus*. Genitalia as shown in Figure 3, more slender in both ventral and lateral views than in *S. brevipennis* or *S. aztecus*; apical enlargement of aedeagus narrower than distance from tip to tip of pointed projections at apex of each digitus; cuspides with relatively short setae, without long hairs.

Vestiture. As in *S. brevipennis.*

Color. Ferruginous and black, extensively marked with yellow.

Head mostly ferruginous, sometimes partly replaced with black especially in specimens from more eastern localities, with yellow markings. Mandibles ferruginous shading to black apically; labial and maxillary palpi yellow suffused with ferruginous. Labrum and clypeus yellow with narrow ferruginous borders apically; supraclypeal area yellow with a ferruginous or black line along posterior margin of clypeus; tentorial pits and lines extending from them to antennal sockets ferruginous, sometimes partly replaced with black, lines to antennal sockets sometimes indistinct. Broad inner orbits to level of midocellus yellow; supra-antennal area between yellow of inner orbits all ferruginous, or all black, or ferruginous with a pair of black spots above antennae, and often with a black spot surrounding the midocellus; area above midocellus and vertex either all ferruginous or partly and sometimes extensively replaced with black; inner orbits above midocellus ferruginous even in darker individuals. Postorbital yellow stripe often present, sometimes restricted to top half of compound eye, and sometimes absent; occiput often entirely ferruginous, sometimes partly replaced with black especially within occipital carina, black sometimes more extensive, occasionally continuous with the vertex which is also black in such melanic individuals. Scape yellow below, ferruginous above; pedicel ferruginous; flagellomere I ferruginous, paler below, and sometimes with a fuscous spot above near apex; flagellomere II often mostly ferruginous; flagellomere XI ferruginous apically and ventrally; remainder of flagellum ranging from ferruginous below and fuscous above to entirely fuscous in darker individuals.

Mesosoma ferruginous, sometimes more or less extensively replaced with black, marked with yellow. Pronotum mostly ferruginous, sometimes partly replaced with black; dorsal margin with a band of yellow which is often wider to each side; pronotal lobes yellow; small yellow spot sometimes present anterior to each pronotal lobe. Scutum with disk ranging from ferruginous, to partly black, to all black in the darkest individuals; broad lateral margins always ferruginous or ferruginous tinged with yellow. Scutellum ferruginous, sometimes with anterior margin black, often with a pair of oblong lateral spots which are sometimes connected medially, occasionally mostly yellow. Metanotum ferruginous, sometimes black anteriorly, with a yellow band which is sometimes interrupted medially. Propodeum ranging from ferruginous, to partly black, to entirely black; yellow spots sometimes present on lateral angles above and within dorsal enclosure laterally. Mesopleura and metapleura ranging from ferruginous to more or less extensively black; very small yellow spot sometimes present behind each pronotal lobe in paler specimens. Coxae entirely ferruginous or black basally; trochanters and femora ferruginous, partly fuscous in darker individuals; tibiae and tarsi ferruginous, sometimes tinged with yellow; claws dark distally. Tegulae and post-tegulae ferruginous, sometimes partly yellow. Veins of

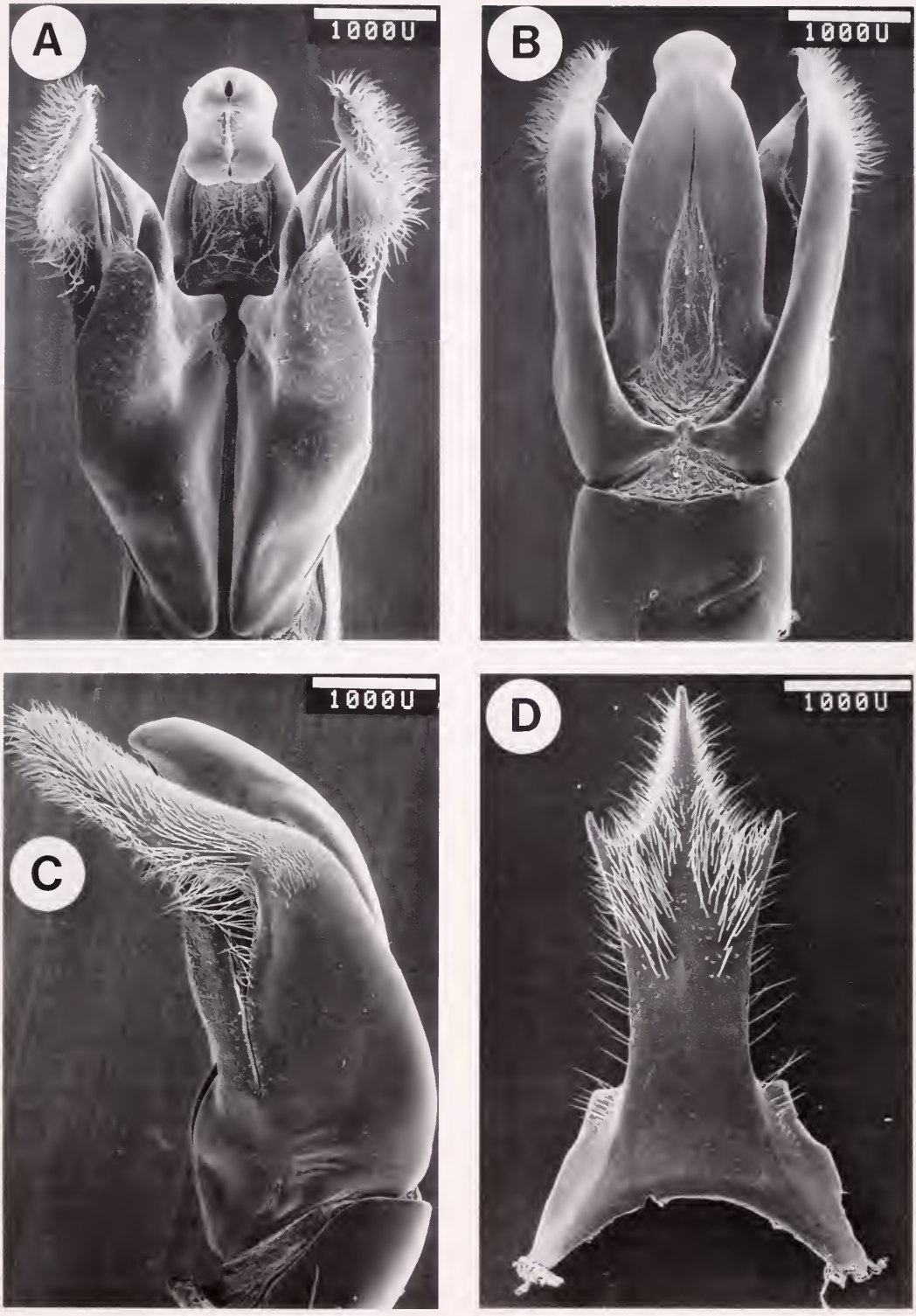

Figure 3. *Stizus texanus* Cresson. Male genitalia in A. dorsal, B. ventral, and C. lateral views; D. male sternum VIII, ventral view.

both wings ferruginous, those surrounding marginal and submarginal cells and both recurrent veins darker, almost brown; membranes of both wings subhyaline, tinged with dark amber, slightly infumate in marginal cell and along transverse cubital veins.

Gaster ranging from ferruginous to extensively dark brown or black, marked with yellow. Terga I to IV with large lateral yellow spots, these widely separated and rounded or subquadrate on terga I and progressively closer together and more elongate on more distal terga, sometimes connected medially on terga III and IV; terga V and VI with or without yellow markings, when present these range from small, widely separated spots to a continuous band of yellow; when the spots on any tergum are joined medially to form a continuous yellow band, the anterior margin of the band deeply and more or less triangularly emarginate medially, and posterior margin nearly straight or only shallowly emarginate medially; tergum VII sometimes tinged with yellow in paler individuals. Sternum II with or without lateral yellow spots of variable size; sterna III and IV always with lateral yellow spots of variable size, sometimes connected medially; sternum V sometimes with small lateral yellow spots.

Female. Similar to male; length 24 to 30 mm.

Structure. Much as in male; frons somewhat wider; clypeus somewhat shorter, more transverse, apical margin nearly straight or with a shallowly rounded emargination; apical flagellomere more evenly curved, apex evenly rounded; scutellum with or without a very shallow median depression. Width across pronotal lobes 6 to 7.5 mm. Forewing length 21 to 23 mm. Apical tergum with a well-defined pygidial plate bordered by carinae; lower margin of tergum VI with basal three fourths nearly straight in lateral view.

Vestiture. As in *S. brevipennis*.

Color. Similar to male, exhibiting a similar range of variation; scutellum apparently always marked with yellow; pygidial plate fuscuous.

Types: Male holotype No. 2054.1 in the collection of the Philadelphia Academy of Natural Sciences. Two additional specimens in the Museum of Comparative Zoology collected by Boll in Dallas, Texas bear type labels No. 512 (1) and No. 512 (2) and may be part of the original series of four specimens studied by Cresson.

Type Locality: Dallas, Texas.

Distribution: *Stizus texanus* is known from southeastern Arizona, New Mexico, Texas, Oklahoma, southwestern Arkansas, and Chihuahua, Mexico. Evans (1966: 125) reported taking this species on flowers of *Baccharis* in Arizona, and data from labels add the genera *Helianthus* and *Asclepias* as nectar sources. Collection dates range from May to September.

I have examined the following specimens, 33 males and 34 females:

ARIZONA: *Cochise Co.*: Douglas, ♀, VIII-12-1936 (W. W. Jones, MCZ): 25 mi NE, ♂, IX-1-1965, on flowers of *Helianthus annuus* L. (J. H. Davidson and M. A. Cazier, UCD). Willcox, 6 mi SW, ♀, VIII-9-1948, on flowers of *Asclepias* (H. E. Evans, MCZ). *Pima Co.*: Tucson, ♀ (G. v. Krockow, AMNH).

ARKANSAS: *Little River Co.*: ♀, VII-2-1944 (UCD).

NEW MEXICO: *Otero Co.*: White Sands National Monument, 2 ♂, ♀ (C. R. Kovacic, D. R. Miller, UCD). *Socorro Co.*: Bernardo, ♂, VII-24-1970 (B. Apperson, BBSL).

OKLAHOMA: *Murray Co.* (?): Arbuckle Mts., 2 ♂, (R. H. Beamer, USNM).

TEXAS: *Bexar Co.*: 7 ♀, V-21-1931, VI-23-1931, VI-14, 22, 23, 26-1932 (H. B. Parks, TA&M); ♂, VI-24-1932 (H. B. Parks, TA&M). San Antonio, 3 ♂, V-27-1927 (USNM); ♂, VI-29-1956 (H. E. Evans, E. G. Matthews, MCZ). *Brewster Co.*: Alpine, ♂, VI-4-1927 (USNM); 32 mi S, ♂, VI-6-1961 (R. Gamez, MCZ). Big Bend National Park, Chisos Mts., 2 ♂, ♀ (J. Bequaert, MCZ). *Crane Co.*: Junction US 80 and farm-road 1053, 3 mi S, ♂, VI-10-1961, on flowers of *Asclepias subverticillata* (J. E. Gillaspy, MCZ). *Dallas Co.*: 9 ♂, 8 ♀ (Boll, MCZ); holotype (Boll, PANS). *Fannin Co.*: Bonham, ♀, VII-2-1936 (TA&M). *Kaufman Co.*: ♀, VII-10-1935 (J. H. Robinson, MCZ). *Lasalle Co.*: Cotulla, ♂, 4 ♀, VI-21-1906 (H. Caley, MCZ). *Webb Co.*: Laredo, 2 ♀, VI-16-1924 (USNM). *Co. unknown*: ♂, ♀ (MCZ).

CHIHUAHUA, MEXICO: Cyn de Bachimba, 27 mi S Chihuahua, ♀, IX-7-1950 (R. F. Smith, AMNH). Hidalgo del Parral, 2 ♀, VII-22-1967 (R. C. Gardner,

C. R. Kovacic, K. Lorenzen, UCD, JWS); 4 ♂, VIII-10-1967 (R. C. Gardner, C. R. Kovacic, UCD, JWS); 9 mi S, ♀, VIII-8-1967 (R. C. Gardner, C. R. Kovacic, K. Lorenzen, UCD). Meoqui, 6 mi NE, 2 ♂, IX-2-1950 (R. F. Smith, AMNH).

Remarks: Stizus texanus occurs in two fairly distinct color phases. Specimens from the eastern portion of the range (southwestern Arkansas, eastern Oklahoma, and eastern Texas) are very dark with the typically ferruginous areas tending to a dark brown, while those from more western localities (most of Texas, New Mexico, Arizona, and Chihuahua) are mostly ferruginous with very little, if any, dark brown and have the yellow maculation more extensively developed. Two males from the Arbuckle Mountains of Oklahoma are interesting in this regard since one is very dark while the other closely approaches the more xanthic coloration exhibited by individuals from the western and more xeric portions of the range. This example of the two color phases occurring in close proximity, together with the fact that various intermediate forms are sometimes encountered, leaves little reason to grant subspecific status to the two color phases.

Stizus aztecus new species

Holotype male: Length 30 mm.

Structure. Very similar to *S. texanus*, differing most concretely in the genitalia. *Head* in facial view with lateral ocelli not projecting above rounded vertex. Clypeus with apical margin evenly rounded, median half not nearly straight; supraclypeal area relatively broad, width/length about 2.76 (measured as in *S. brevipennis*); median frontal depression surrounding midocellus. Flagellum without tyloids; apical flagellomere distinctly emarginate within, apex more angulate than in *S. texanus*.

Mesosoma robust; width across pronotal lobes 7 mm. Scutum without evident notauli; admedian lines carinate throughout; parapsidal lines faint, not reaching posterior margin of scutum; posterior margin of scutal lamina produced into a distinct lobe behind oblique scutal carina; propodeum with a pair of carinae on lower posterior surface extending upward from submarginal sulcus. Forewing length 22 mm.

Gaster robust, more inflated than in *S. texanus*. Tergum VII and sternum VI as in *S. texanus*; sternum VII somewhat broader and more distinctly emarginate apically than in *S. texanus*; sternum VIII as shown in Figure 4, more robust than in *S. texanus*. Genitalia as shown in Figure 4, more robust than in *S. texanus*, longitudinal axis clearly oblique to basal margin; apical enlargement of aedeagus wider than distance from tip to tip of the two pointed projections at apex of each digitus; cuspides with short setae, without long hairs.

Vestiture. As in *S. brevipennis*.

Color. Black and ferruginous marked with whitish yellow. *Head* mostly ferruginous; clypeus whitish yellow bordered apically with a narrow band of ferruginous; supraclypeal area whitish yellow; line along posterior margin of clypeus ferruginous; tentorial pits and lines extending from them to antennal sockets black bordered by ferruginous; inner orbits to near level of midocellus whitish yellow; supra-antennal area ferruginous with a black spot adjacent to each antennal socket; frons above midocellus and vertex ferruginous; occiput ferruginous, black within and slightly beyond occiptal carina; genae ferruginous. Mandibles ferruginous with distal half black. Scape and pedicel ferruginous; flagellomere I ferruginous with a fuscous stain above distally; apical flagellomere ferruginous at apex and along ventral surface; remainder of flagellum fuscous.

Mesosoma black and ferruginous marked with whitish yellow; pronotum ferruginous shading to black anteriorly, spot on pronotal lobe whitish yellow; scutum ferruginous laterally, posterior margin and much of disk black nearly surrounding a pair of lanceolate, ferruginous

spots; scutellum ferruginous, lateral declivities darker; metanotum ferruginous; propodeum, metapleura, and metasternum black; mesopleura mostly black with spot behind pronotal lobe and lobes between mesocoxae ferruginous. Tegulae and axillary sclerites ferruginous. Wings subhyaline tinged with dark amber, slightly smoky; marginal cell with anterior half infumate; veins ferruginous, costal vein darker distally, almost brown. Coxae and trochanters black distally shading to ferruginous on lower surface; femora ferruginous with small amount of black basally; remainder of leg ferruginous; claws dark apically.

Gaster black and ferruginous marked with whitish yellow. Terga I to V with lateral whitish yellow spots, those on tergum I subcircular, those on tergum II ovate, and those on succeeding terga progressively narrower; lateral spots widely separated medially on tergum I and progressively closer together, but not joined medially, on succeeding terga; remainder of dorsal surface of gaster black except for ferruginous area between lateral spots on tergum I. Sterna black, narrowly ferruginous along apical margin of sternum I; sterna III and IV with widely separated, subcircular spots, spots larger on sternum III than on sternum IV. Genitalia brown, clearly darker than in *S. texanus*.

Allotype female: Similar to male; length 27 mm.

Structure. Difficult to distinguish from *S. texanus*. Clypeus somewhat more rugose medially above apical margin and lamellate apical border wider than in *S. texanus*. Dorsal ridge of pronotum with median indentation deeper than in *S. texanus*. Bulge in metapleuron adjacent to insertion of hindwing with two strong transverse carinae in *S. texanus*, and with lower carina poorly developed in *S. aztecus*. Ridge along lower margin of propodeum from midcoxa to bulge at base of hindcoxa carinate and extending onto bulge in *S. texanus*, and more rounded and not extending onto bulge in *S. aztecus*. This ridge forms lower margin of a triangular enclosure bordered above by a ridge extending from metapleuron to bulge at base of hindcoxa. The upper ridge is simply carinate in *S. texanus*, and in *S. aztecus* it is lower, broader, and (usually) bicarinate anteriorly. Width across pronotal lobes 6.5 mm. Forewing length 20 mm.

Vestiture. As in *S. brevipennis*.

Color. As in holotype male with the following differences. *Head* with supraantennal area ferruginous without black spots; area within occipital carina partly ferruginous, black not extending beyond carina. *Mesosoma* predominantly ferruginous; pronotum with black reduced to two small areas on each side, dorsal margin narrowly whitish yellow; scutum ferruginous except for narrow black area along median third of anterior margin; propodeum ferruginous with black restricted to line along anterior margin, most of lateral surface, posterior apex of enclosure, and lower margin of posterior face; metapleuron black with central ferruginous spot; mesopleuron ferruginous over most of lateral surface and along midline below with most of ventral surface and along sutures black, coxae and trochanters more extensively ferruginous.

Gaster with ferruginous more extensive; terga I to IV partly ferruginous; sterna II and III largely ferruginous, sterna IV and V less extensively so.

Variation: The paratypes agree in most respects with the description of the holotype but exhibit considerable variation in color and size. Color variation is much the same in the two sexes, and there is no consistent color dimorphism. The most striking variation concerns the relative extent of black and ferruginous. The lightest individuals approximate the condition in the allotype female, and the darkest individuals differ from the holotype as follows: Head with black extending from antennal sockets to vertex forming a band of width subequal to distance between the outer margins of the antennal sockets; occiput

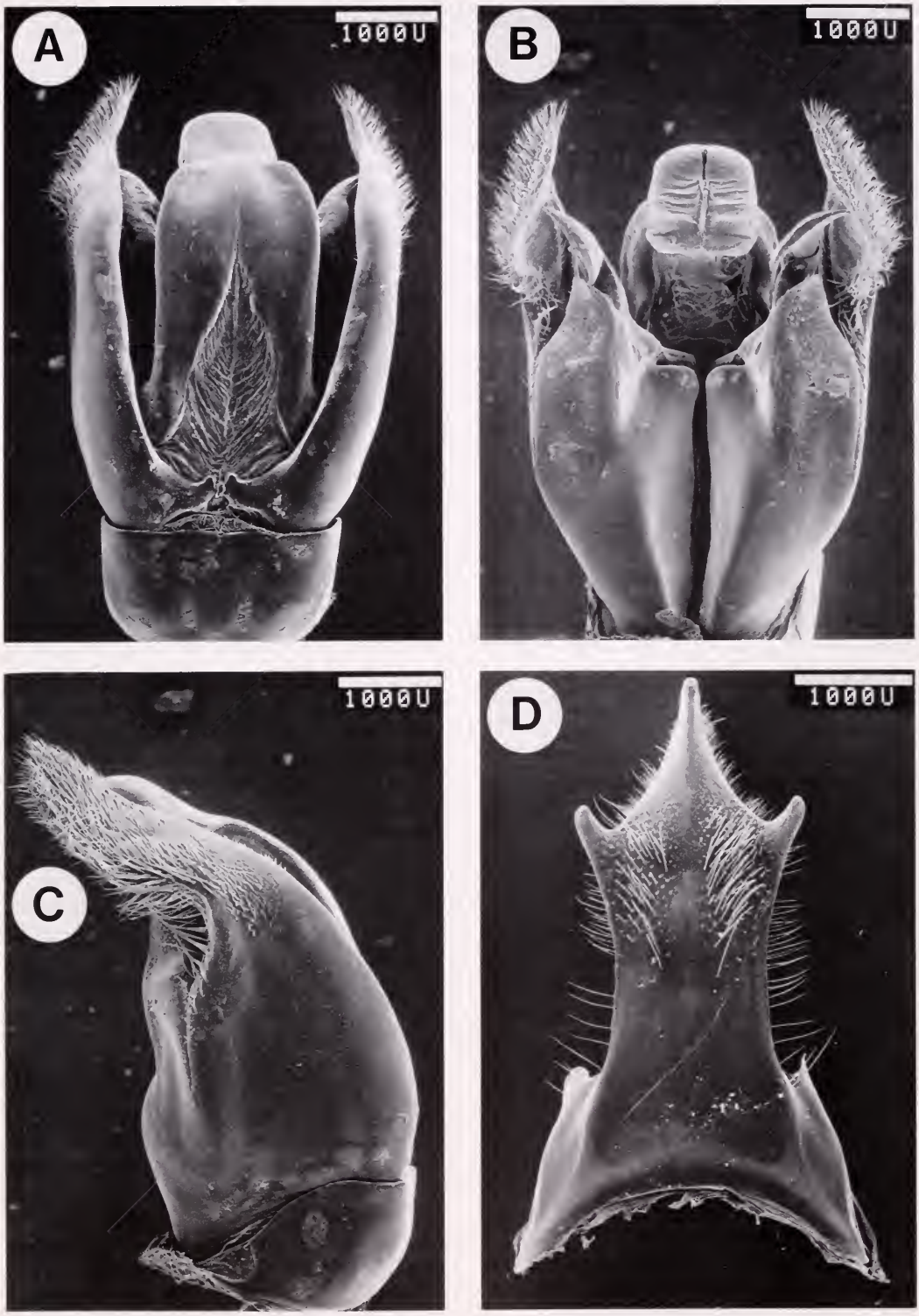

Figure 4. *Stizus aztecus,* new species. Male genitalia in A. dorsal, B. ventral, and C. lateral views; D. male sternum VIII, ventral view.

with black extending well beyond occipital carina and joining band extending from the antennal sockets. Mesosoma black with ferruginous much reduced; pronotum black, narrowly ferruginous along borders; scutum mostly black, ferruginous along lateral margins; scutellum mostly ferruginous, black laterally and along sutures; propodeum, metapleuron, and mesopleuron entirely black; coxae and trochanters almost entirely black; femora partly black, especially on hind legs. Gaster with background black, virtually without ferruginous. There is also considerable variation in the size of the whitish yellow maculations, and those on the sterna are sometimes virtually absent. The holotype is unique in lacking a band of whitish yellow along the dorsal margin of the pronotum. Unlike *S. texanus*, none of the available specimens of *S. aztecus* have any yellow on the scutellum. Male dimensions are: length 28 to 33 mm, width across pronotal lobes 6.5 to 8 mm, and forewing length 21 to 23 mm; the equivalent measurements for females are 26 to 28 mm, 6 to 7.5 mm, and 19.5 to 22 mm, respectively.

Types: Holotype male and allotype female, collected IX-22-1955 by G. E. Bohart on *Baccharis glutinosa* in Bisbee, Cochise Co., Arizona, to be deposited in the collection of the University of California at Davis. Paratypes, 4 males and 3 females, as follows:

CHIHUAHUA, MEXICO: 2 miles SE Temoris (actually Temores according to maps I have consulted, a town about 200 miles west of Hidalgo del Parral), ♂, 2 ♀, IX-11-1969 (T. A. Sears, R. C. Gardner, C. S. Glaser, UCD, JWS).

NAYARIT, MEXICO: Tepic, ♀, VIII-22-1905 (P. H. Goldsmith, MCZ). 25 miles NW Tepic, ♂, X-8-1950 (R. F. Smith, AMNH).

The two remaining male paratypes were purchased years ago by R. M. Bohart (personal communication) from the H. S. Gentry collection and bear the confusing locality record: "Mesa Col[orada?]. Son. Chih." I have been able to locate two settlements bearing the name Mesa Colorado (26°54'N, 108°14'W and 27°56'N, 108°38'W) both within the boundaries of Chihuahua and both within the region delimited by other localities where *S. aztecus* has been collected. It is probable that the specimens come from one or the other of these two places. Both specimens are in the UCD collection; one bears the date VIII-25-1933 and the other X-20-1933.

Remarks: *Stizus aztecus* is very closely related to *S. texanus*, but the genitalic differences are striking and constant. The females of the two species are difficult to separate on structural grounds, and the differences cited above may prove inadequate when more material becomes available. Similarly, the color of the scutellum which I rely on to separate females in the key may also prove inadequate. It should be noted, however, that the two species are strikingly different in color in Chihuahua and southeastern Arizona where they occur in close proximity. *S. aztecus* is marked with whitish yellow on a very dark, mostly black, background while western individuals of *S. texanus* are much more extensively marked with a deeper shade of yellow on an almost entirely ferruginous background. Darker individuals of *S. texanus* from more eastern localities are more difficult to distinguish from *S. aztecus*, but this problem should not arise in practice. It may also be noted that the two species appear to have different ecological requirements, and no cases of local sympatry are now known. *S. aztecus* is a montane form apparently restricted to the Sierra Madre Occidental and its outliers while *S. texanus* is largely a lowland form occurring east of the Mexican cordillera and north to Oklahoma and southeastern Arkansas with a western extension into the lowlands of southeastern Arizona.

Stizus occidentalis Parker

1929 *Stizus occidentalis* Parker, Proc. U.S. Nat. Mus. **75**(5): 9–10, pl. 4, fig. 29.

1942 *Stizus occidentalis* Parker. Dow, Psyche, **48**: 176, figs. 2, 4.

1943 *Stizus occidentalis* Parker. Lohrmann, Mitt. Munchn. Ent. Ges. **33:** 195.

Male: Length 16 to 21 mm.

Structure. Head in facial view with posterior ocelli distinctly projecting above the nearly straight vertex. Clypeus emarginate apically, posterior margin nearly straight. Antennal sockets separated from eyes by somewhat less and from each other by somewhat more than their transverse diameter; space between antennal sockets with a low ridge, carinate posteriorly. Median frontal depression narrower than in *S. iridis*, not surrounding anterior ocellus; lateral margin of each posterior ocellus bordered by a longitudinal, shining impression about one third the diameter of the ocellus in width and extending posteriorly for a distance about equal to the diameter of the ocellus but not descending the vertical face of the occiput. Flagellomeres VII to X much shorter than the four preceding; apical flagellomere rather variable in shape, apex evenly rounded to obliquely truncate when viewed from the direction of the tyloidal surface; linear tyloids present on flagellomeres V to XI, that on apical flagellomere longer than in *S. iridis*, usually more than half as long as the flagellomere.

Mesosoma in dorsal view more rounded anteriorly and more pointed behind than in *S. iridis*; width across pronotal lobes 4.5 to 5.5 mm; parapsidal furrows not extending to posterior margin of scutum, represented by simple impressed lines; oblique scutal carina present, delimiting a posterolateral declivity nearly at the posterior margin of the scutum, declivity almost vertical with posterior margin only slightly produced into a lobe; posterior angles of propodeum not as convex as in *S. iridis*; propodeum without a pair of carinae on lower posterior face. Forewing length 13.5 to 16 mm; first transverse cubital vein nearly straight. Legs not as slender as in *S. iridis*; foretarsal rake poorly developed.

Gaster somewhat more inflated than in *S. iridis*; tergum I with convex sides as seen from above, distinctly rounded anteriorly in dorsal aspect, and with a less sharply marked anterior face than in *S. iridis*; sternum VII with a prominent longitudinal carina on the inner surface extending from the basal carina for about three fourths the length of the sternum; sternum VIII as shown in Figure 5; median prong not as long as in *S. iridis*. Genitalia as in Figure 5; compressed shaft of digitus in lateral view about the same width throughout; cuspides long and slender, rounded apically; parameres exceeding aedeagus by less than length of apical enlargement of aedeagus.

Vestiture. Conspicuous pale hairs up to four midocellus diameters in length on vertex, lower genae, mesosoma, and tergum I, but shorter and often not as dense on remainder of body. Coxae, trochanters, and femora with erect hairs. Short, appressed pubescence restricted to legs, tegulae, sclerites at base of wings, and the larger veins of both wings. Membranes of both wings with widely spaced setae, these much sparser than in *S. iridis*, denser near the anterior margins, absent from posterior portions of first and second submarginal cells and from most of the median cell of the hindwing.

Color. Black and ferruginous, extensively marked with yellow.

Head black marked with yellow; labrum, clypeus, supraclypeal area except for dark stains marking tentorial pits, and inner orbits to level of midocellus all yellow. Upper frons (between antennal sockets and midocellus) with yellow of variable extent; typically, a pair of black spots present above antennae, these usually joined medially and extending upward to black area above midocellus and thereby surrounding a pair of crescent-shaped yellow spots separated medially by a narrow wedge of black extending downward from midocellus; occasionally, the supra-antennal black spots completely surrounded by yellow and rarely the upper frons entirely black except for the inner orbits. Scape yellow with a black spot above and usu-

ally tinged with ferruginous, especially above. Flagellum fuscous and orange-ferruginous; flagellomeres I to III and XI usually all or mostly orange-ferruginous and others fuscous, occasionally the orange more extensive, sometimes extending to lower surface of all flagellomeres and, in other cases, fuscous more extensive, extending to the dorsal surface of all flagellomeres. Postocular stripe always present, yellow, narrower above, and separated from eye by a narrow black line. Mandibles yellow, dark apically. Labial and maxillary palpi yellow, more or less suffused with ferruginous. Compound eyes pale brown.

Mesosoma mostly black. Pronotum yellow, black anteriorly; anterior black area often with a pair of rectangular posterior projections above; black spot present near each pronotal lobe, this usually connected both above and below to the anterior black area. Scutum black with yellow-ferruginous lateral margins. Tegulae and base of wings ferruginous. Scutellum black, usually with lateral semicircular yellow spots narrowly separated medially, spots sometimes joined medially, yellow occasionally absent. Metanotum often entirely black, sometimes with lateral oblong yellow spots which occasionally meet medially. Mesopleuron with a small yellow spot near pronotal lobe, this spot sometimes inconspicuous or absent. Legs mostly yellow, more or less suffused with ferruginous especially at the joints between segments; coxae black with a variable amount of ferruginous ventrally and distally; trochanters ferruginous, sometimes black basally; femora ferruginous, usually more or less yellow beneath; claws dark apically. Forewing with marginal cell strongly infumate, darker in the anterior half; central portion of forewing suffused with amber, basal and distal portions clear; entire hindwing clear; veins of both wings ferruginous, those surrounding marginal cell darker, almost brown.

Gaster mostly yellow with black and ferruginous markings. Anterior face of tergum I black, often more or less replaced with ferruginous along posterior margin, and usually with three posterior extensions. Anterior margin of each succeeding tergum black, sometimes more or less replaced with ferruginous, with a medial triangular extension sometimes extending to the apical margin as a faint line. Terga I to VI with apical translucent ferruginous bands, these sometimes narrowly interrupted medially. Tergum VII extensively black anteriorly with an apical yellow band narrowly bordered with ferruginous; spiracular lobes black with a rather broad partially transparent yellow margin apically and ventrally. Sterna I to VI black basally, often more or less extensively replaced with ferruginous; black area with rounded triangular posterior extension medially, this more or less continuous with translucent ferruginous apical bands and thus more or less distinctly defining the medial borders of a pair of lateral yellow spots, except on sternum I which is extensively ferruginous and without yellow. Sternum VII black basally and extensively ferruginous apically. Sternum VIII dark brown basally with ferruginous prongs. Genitalia more heavily pigmented than in *S. iridis*, brown.

Female: Similar to male, usually larger, length 16 to 21 mm.

Structure. As in male aside from the usual sexual differences and the following exceptions: antennae without tyloids; width across pronotal lobes 4.5 to 6 mm; forewing length 13 to 17 mm; foreleg with well-developed foretarsal rake. Apical tergum without a pygidial plate.

Vestiture. As in male.

Color. Similar to male; yellow areas usually more extensive and black areas often replaced with ferruginous; black spots above antennae smaller, not joined medially, and not extending to black area on vertex; antennae more extensively orange-ferruginous, fuscous restricted to dorsal portions of pedicel and flagellomeres V to VII or less; black on pronotum often much reduced; scutellum mostly

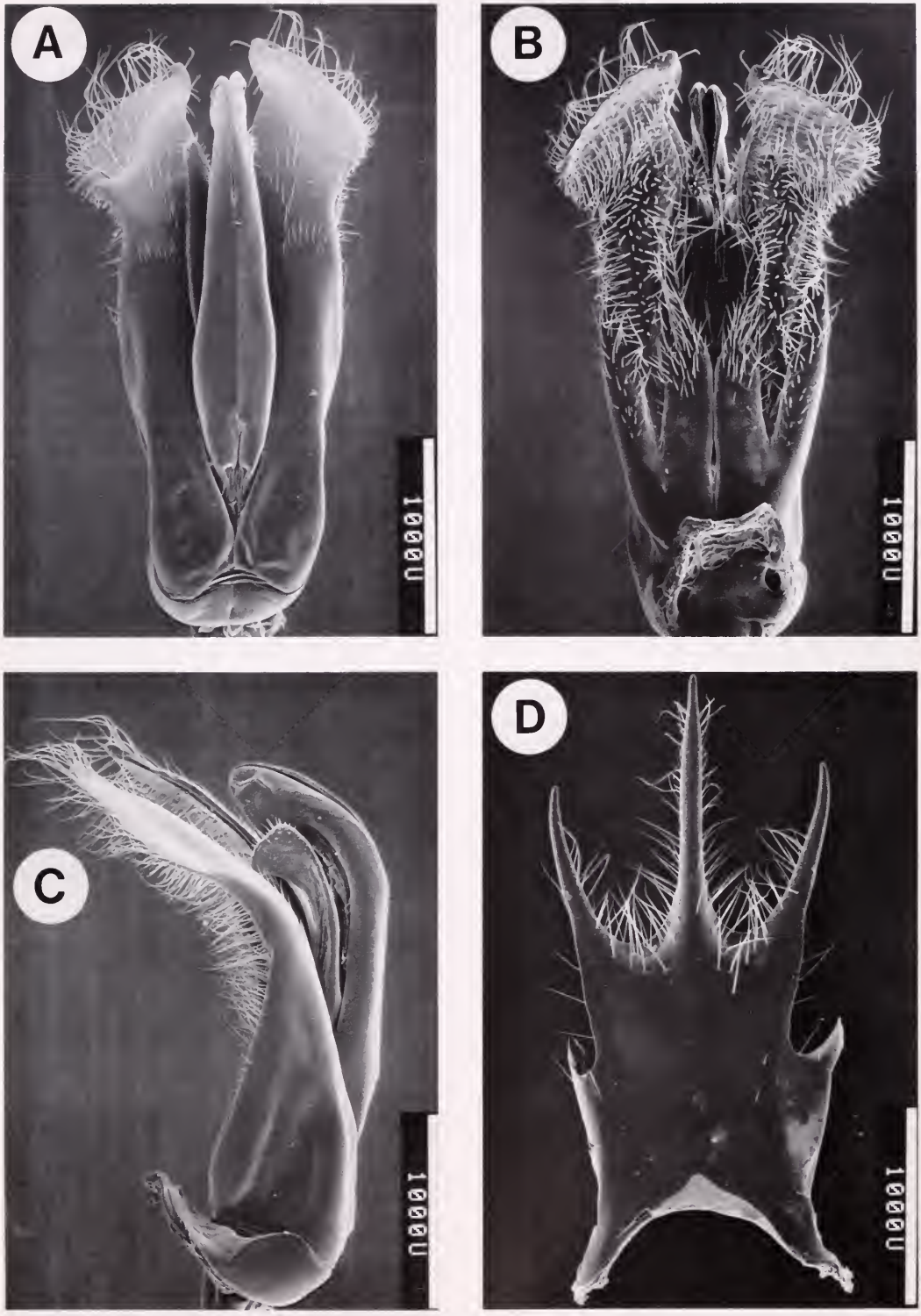

Figure 5. *Stizus occidentalis* Parker. Male genitalia in A. dorsal, B. ventral, and C. lateral views; D. male sternum VIII, ventral view.

yellow; spots of yellow or ferruginous on posterior face of propodeum sometimes present.

Types: Holotype male Cat. No. 40847, U.S. National Museum. Allotype female in the collection of the Philadelphia Academy of Natural Sciences.

Type Locality: "Described from two specimens, a male from San Diego County, California, collected by Mr. Coquillett, and a female from Florence, Arizona" (Parker, 1929). Dow (1942) has suggested that the holotype male "may really have been taken in what is now Imperial County, formerly the eastern part of San Diego County." In any event, *S. occidentalis* is now known from both San Diego and Imperial Counties.

Distribution: *Stizus occidentalis* has previously been recorded from California and Arizona, and the range is here extended to include southern Nevada and Utah. Floral records include *Acacia*, *Dalea*, *Pluchea*, *Prosopis*, *Sarcostemma*, and *Tamarix*. Collection dates range from March to July. I have examined the following specimens, 84 males and 42 females:

ARIZONA: *Coconino Co.*: Grand Canyon, Mile 52, ♂, VI-6-1953 (G. D. Butler, USNM). Grand Canyon National Park, 15 mi NE Phantom Ranch, ♂, V-1-1968 (J. E. Slansky, UCD). *Mojave Co.*: Cattail Cove, 9 mi N Parker Dam, ♂, IV-7-1972, on flowers of *Tamarix gallica* (B. Apperson, BBSL). Lake Havasu City, ♀, IV-28-1972 (P. Torchio, G. Bohart, and F. Parker, BBSL). *Maricopa Co.*: Gila Bend, 18 mi S, ♂, V-8-1965, on flowers of *Prosopis glandulosa* Torr. (M. A. Mortenson, J. M. Davidson, and M. A. Cazier, UCD). *Pima Co.*: Ajo, 3 mi S, ♂, IV-22-1966, at flowers of *Prosopis* (Torchio, Rust, and Yousef, BBSL). *Pinal Co.*: Florence, allotype ♀, V-20-1903 (PAS). *Yuma Co.*: Yuma, 45 mi N, ♀, IV-5-1972 (W. Apperson, BBSL).

CALIFORNIA: *Imperial Co.*: Glamis, on dunes, ♂, IV-20-1978 (J. W. Stubblefield, JWS). *Inyo Co.*: Ballarat, ♂, III-26-1961 (D. R. Miller, UCD); ♂, ♀, III-27-1972, on flowers of *Prosopis glandulosa* Torr. (J. D. Pinto, UCR). Darwin Falls, ♀, V-8-1958 (R. M. Bohart, UCD); 5 ♂, V-8-1958 (A. E. Menke, UCD); ♂, V-8-1958 (A. E. Menke, LACM); ♀, V-8-1958 (L. A. Stange, UCD); ♀, V-6-1961 (F. D. Parker, UCD); ♂, V-21-1965 (A. S. Menke, UCD); 7 ♂, IV-9-1972 (G. E. Bohart, UCD). Death Valley Junction, 3 mi W, ♂, V-17-1970 (R. M. Bohart, UCD). Furnace Creek, Death Valley, ♂, III-25-1961 (V. L. Vesterby, UCD). Grotto Canyon, Death Valley, 2 ♂, ♀, IV-22, 23-1976 on flowers of *Sarcostemma hirtellum* (Gray) (J. W. Stubblefield, JWS). Mormon Hill, Death Valley, 3 ♂, III-25-1961 (V. L. Vesterby, UCD); 4 ♂, III-29-1961 (M. E. Irwin, UCD). Panamint Mountains, ♂, V-28-1937 (C. D. Michener, MCZ); 2 ♀, V-29-1937 (N. W. Frazier, MCZ). Panamint Valley, 3 ♀, V-1, 2-1976 (J. W. Stubblefield, JWS). Post Office Spring (near Ballarat), 1,080 ft, ♀, IV-9-1972, on flowers of *Prosopis glandulosa* Torr. (J. W. Stubblefield, JWS). Saline Valley, Morning Sun Mill Site, ♀, IV-21-1973 (G. W. Akin, JWS). Saratoga Spring, Death Valley, 2 ♂, III-30-1956 (Belkin and MacDonald, LACM); 2 ♂, III-29-1961 (R. D. Nelson, LACM); 2 ♂, 2 ♀, III-30-1961 (D. R. Miller, UCD); ♂, ♀, III-30-1961 (V. L. Vesterby, UCD); ♀, V-20-1965 (A. S. Menke, L. A. Stange, UCD). Stovepipe Wells, on nearby dunes, ♀, IV-23-1976, on flowers of *Prosopis glandulosa* Torr. (J. W. Stubblefield, JWS). Surprise Canyon, Panamint Mts., 10 ♂, 7 ♀, V-9-1958 (R. M. Bohart, UCD); 5 ♂, ♀, V-9-1958 (A. E. Menke, UCD); ♀, V-9-1958 (A. E. Menke, LACM); 4 ♂, ♀, V-9-1958 (L. A. Stange, UCD); 3 ♂, V-9-1958 (M. A. Stange, UCD). Wild Rose, Panamint Mts., ♀, V-20-1937 (UCD). *San Bernardino Co.*: Cronise Valley, 3 ♀, V-5-1960 (F. D. Parker, UCD). Salt Creek (north of Baker), ♀, V-7-1973, on flowers of *Prosopis glandulosa* Torr. (J. W. Stubblefield, JWS); 2 ♂, V-7-1973, on flowers of *Tamarix* (J. W. Stubblefield, JWS); 3 ♀, IV-23, 24-1976, on flowers of *Prosopis glandulosa* Torr. (J. W. Stubblefield, JWS); 2 ♀, IV-23-1978, on flowers of *Prosopis glandulosa* Torr. (J. W. Stubblefield, JWS). *San Diego Co.*: Borrego, ♂, IV-20-1951 (C. D. MacNeill, MCZ).

NEVADA: *Clark Co.*: Glendale, 20 mi W, ♀, VI-2-1973 (P. F. Torchio, BBSL); 2 ♂, IV-29-1975 (F. Parker and P. Torchio, BBSL). Moapa, 7 mi NW, ♂, on flowers of *Prosopis* (R. C. Bechtel, USNM). Valley of Fire, ♂, IV-29-1982, at flowers of *Dalea* (P. F. Torchio, BBSL).

UTAH: *Emery Co.*: Buckskin Spring N of Goblin Valley, 5,100 ft, ♂, VI-14-1983 (T. L. Griswold, BBSL); 3 ♂, VI-15-1983, at flowers of *Tamarix* (J. W. Stubblefield, JWS). North Temple Wash, San Rafael Desert, 5,100 ft, ♂, VI-15-1983, at flowers of Tamarix (J. W. Stubblefield, JWS). Wild Horse Creek N of Goblin Valley, 4,900 ft, ♂, VII-25 to 28–1983 (F. D. Parker and T. L. Griswold, BBSL). Woman Wash, San Rafael Desert, 5,000 ft, 4 ♂, VI-15-1983 (T. L. Griswold, BBSL); 3 ♂, (J. W. Stubblefield, JWS). *Washington Co.*: St. George, ♀, VI-23-1961 (G. F. Knowlton, UCD).

Remarks: *Stizus occidentalis* is closely related to *S. iridis* but is easily separated by its mostly black mesosoma. Both are desert species and inhabit similar ranges, but *S. occidentalis* flies earlier in the year and mostly at lower elevations than *S. iri-*

dis. S. occidentalis is by far the most frequently collected western species and is often common about the flowers of *Prosopis* during March, April, and May in the Death Valley region of eastern California.

Stizus iridis Dow

1942 *Stizus iridis* Dow, Psyche **48:** 171–176, 180 (key), figs. 1, 3, 5. ♂.
1976 *Stizus iridis* Dow. Dow, Proc. Ent. Soc. Washington, **78:** 65–66. Nest and prey.

The following description has been extensively modified from Dow (1941) in order to include additional characters and such variation as I have observed. A description of the female appears here for the first time.

Male: Length 20 to 25 mm.

Structure. Head in facial view with the lateral ocelli clearly projecting above the nearly straight vertex. Compound eyes nearest to each other where they meet the clypeus. Clypeus emarginate anteriorly and distinctly but shallowly so posteriorly; supra-clypeal area posteriorly about three times as broad as long. Antennal sockets separated from the compound eyes and from each other by somewhat less than their transverse diameter; space between antennal sockets with a low ridge, more or less carinate posteriorly. Median frontal depression broad, surrounding anterior ocellus; lateral ocelli separated from the eyes by one and one half times their diameter, and from each other by twice their diameter: posterolateral margin of each lateral ocellus bordered by an impressed line which continues posteriorly in a medially concave curve to the vertical face of the occiput. Flagellomeres VII to X much shorter than the four preceding; flagellomere VII about two-thirds as long as VI; apical flagellomere tapering to a rounded apex and not emarginate within: tyloids present as linear carinae on flagellomeres IV to XI, that on III very short, practically a tubercle.

Mesosoma more angulate anteriorly and broader behind in dorsal view than in *S. occidentalis*; width across pronotal lobes 6 to 6.5 mm. Parapsidal lines not extending to the posterior margin of the scutum, each represented by a very slender carina beside an extremely fine impression; oblique scutal carina present, delimiting a posterolateral declivity distinctly anterior to posterior margin of scutum, declivity largely horizontal with posterior margin produced into a distinct lobe. Propodeum without a pair of carinae on lower posterior face. Forewing length 17 to 18 mm; first transverse cubital vein practically straight. Legs more slender than in *S. occidentalis*; foretarsal rake poorly developed.

Gaster with tergum I flattened anteriorly, roundly angulate anteriorly in dorsal aspect, the concave sides parallel towards base as seen from above, diverging posteriorly. Sternum VII with a prominent median longitudinal carina on the inner surface extending from the basal carina for about three fourths the length of the sternum, visible externally as a fine ferruginous line; sternum VIII as in Figure 6, median prong longer than in *S. occidentalis*. Genitalia as in Figure 6; compressed shaft of digitus in lateral view strongly emarginate on ventral margin; cuspides long and slender, rounded apically; parameres exceeding apex of aedeagus by more than length of apical enlargement of aedeagus.

Vestiture. Shorter and less conspicuous than in *S. occidentalis*; pale hairs generally distributed, longer than elsewhere on posterior half of clypeus, sides of the supraclypeal area, anterior portion of supraantennal area, vertex and adjacent occiput, lower portions of genae, lower lateral and ventral portions of mesopleura, posterior angles of the propodeum, and tergum I. Appressed pubescence restricted to legs, tegulae, axillary sclerites, and larger veins of both wings. Membranes of both wings with numerous setae which tend to be denser near the costal margins, but absent from the posterior portion of the sec-

ond submarginal cell and adjacent portions of neighboring cells.

Color. Yellow marked with black and ferruginous.

Head yellow with the following exceptions: mandibles dark brown at apex with a ferruginous line along inner margin; a dark spot above each antenna, variable in size, often inconspicuous and sometimes absent; transverse black band on vertex, variable in width, sometimes shading to ferruginous laterally, sometimes not quite reaching compound eyes, sometimes with anterior pointed extensions laterally; a pair of black or ferruginous bands on occiput connecting sides of transverse band on vertex with an extensive black area surrounding occipital foramen, bands sometimes poorly developed or absent; ferruginous extensions of variable intensity extending posteriorly from lateral ocelli sometimes present. Antennae with scape above, pedicel, and flagellum ferruginous; flagellum shading to black above and to orange toward apex.

Mesosoma mostly yellow. Pronotum with a black transverse band anteriorly, sometimes shading to ferruginous laterally. Disk of scutum and anterior margin between pronotal lobes black, marked with two narrow yellowish longitudinal stripes, or two large spots of reddish brown, or various intermediate patterns, or simply black. Anterior margin of propodeum with a narrow black band, somewhat variable in width, and often with a pointed median extension: sutures of propodeum marked with black lines, sometimes partly obsolete, these meet on posterior surface at a black line extending upward along the median groove. Propleura ranging from black with a small yellow spot near forecoxa to mostly yellow. Ventral portion of mesopleura with a large dark spot, varying from black to partly or entirely ferruginous, often interrupted medially, rather variable in shape, narrowly separated posteriorly from a dark spot near ventral end of the meso-metapleural suture; remainder of mesopleura, except dorsally, suffused with orange of variable intensity. Meso-metapleural and metapleural-propodeal sutures marked with black lines. Metasternum yellow with black markings of variable shape and extent. All coxae black basally, at least anteriorly, sometimes shading to ferruginous; remainder of legs partly suffused with orange. Forewing with veins and membrane yellowish basally, and somewhat ferruginous in the region of the first submarginal and marginal cells, the latter with a dark streak in the anterior half; hindwing yellowish.

Gaster mostly yellow; tergum I with anterior face more or less ferruginous, with a black basal portion usually with a narrow median projection and broad lateral extensions, sometimes lateral or median extensions poorly developed or absent; apical and to some extent lateral margins of all terga orange; basal margins of terga II to V orange or black (always black on terga IV and V) each with a triangular median extension of the same color. Sterna variously marked with orange and black. Genitalia yellowish.

Female: Similar to male, usually larger, length 21 to 28 mm.

Structure. As in male, aside from the usual sexual differences and the following exceptions: supraclypeal area relatively shorter; compound eyes nearest to each other above the clypeus, antennae without tyloids; foretarsal rake well developed. Width across pronotal lobes 6 to 6.5 mm; forewing length 18 to 21 mm. Apical tergum without pygidial plate.

Vestiture. As in male.

Color. As in male with the following exceptions: black on vertex sometimes replaced with ferruginous, lateral margins usually ferruginous; black area surrounding occipital foramen reduced, lateral connections with vertex absent, faint posterior projections from lateral ocelli sometimes present; flagellum more extensively orange, sometimes entirely so; scutum

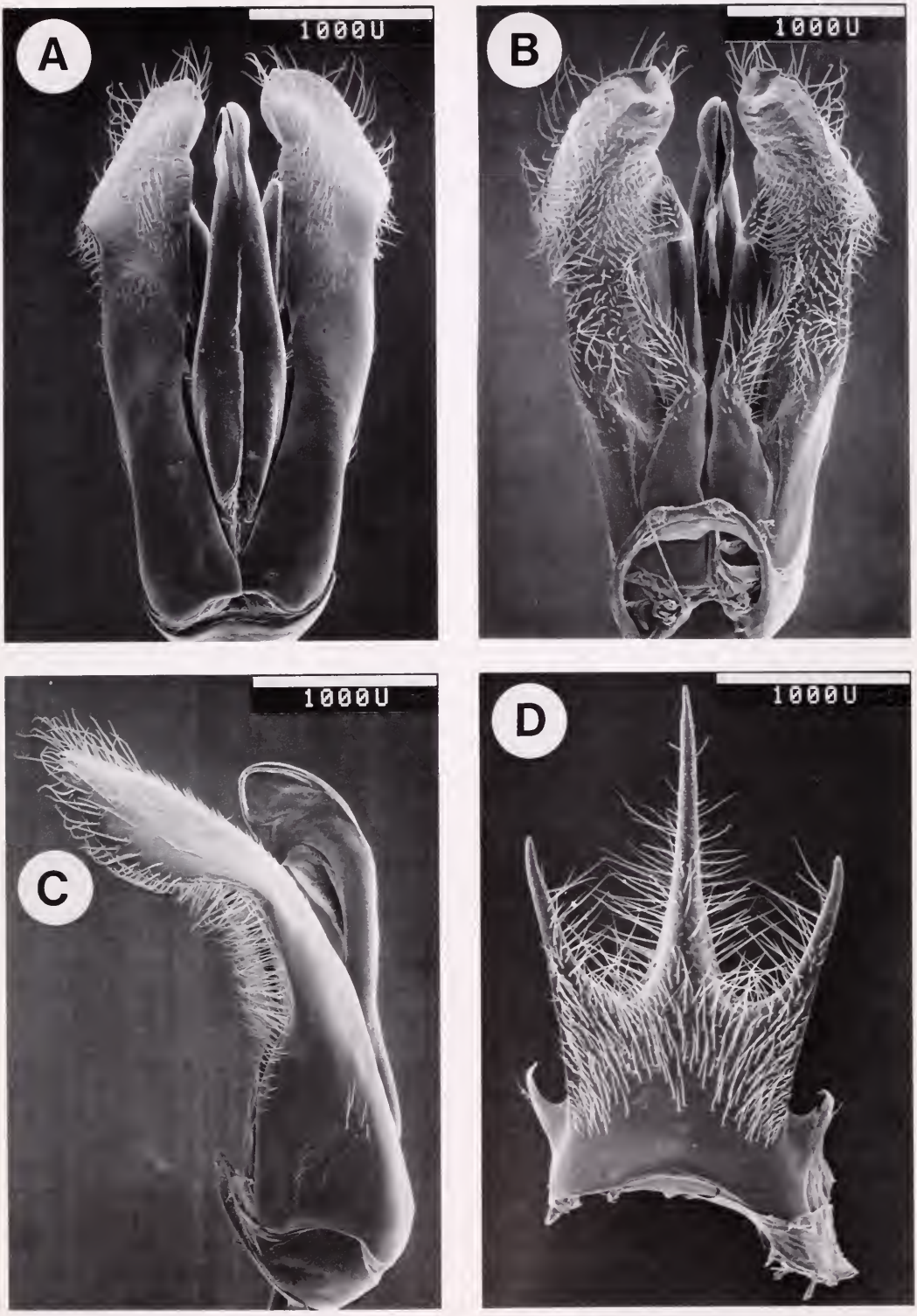

Figure 6. *Stizus iridis* Dow. Male genitalia in A. dorsal, B. ventral, and C. lateral views; D. male sternum VIII, ventral view.

never entirely black; propleura more extensively yellow, black sometimes replaced with ferruginous; mesopleura with black much reduced or absent, often entire ventral portion suffused with orange; black lines marking meso-metapleural and metapleural-propodeal sutures sometimes partially obsolete; black of metasternum replaced with ferruginous; dark streak in anterior half of marginal cell occasionally not evident; black area of tergum I often much reduced; black on sterna often reduced or absent.

Types: Male holotype No. 23397 and male paratype in the Museum of Comparative Zoology, Harvard University. One male paratype, No. 55828, in the U.S. National Museum.

Type Locality: Cited as Rainbow Bridge National Monument, San Juan County, Utah in Dow (1942) and the types bear this locality. Dow (1976), however, relocated the type locality and found it to be on the Navajo Indian Reservation one half mile NNE of Rainbow Bridge, clearly beyond the boundaries of the National Monument.

Distribution: *Stizus iridis* has been previously recorded only from the type locality in Utah, and the range is here extended to include portions of Arizona and California. Collection dates range from July to September, and floral records include the genera *Asclepias*, *Clematis*, *Melilotus*, and *Tamarix*.

I have examined the following specimens, 11 males and 7 females:

ARIZONA: *Coconino Co.*: Cliff Dwellers Lodge, ♂, VII-8-1967, on flowers of *Tamarix pentandra* Pall (J. H. Davidson, J. M. Davidson, M. A. Cazier, UCD).

CALIFORNIA: *Inyo Co.*: Antelope Spring, ♀, VII-16-1960 (H. K. Court, UCD); ♀, VIII-11-1960 (H. K. Court, UCD). Bishop, 15 mi N, ♂, VIII-5-1948 (P. D. Hurd and J. W. MacSwain, MCZ). Limekiln Spring, Surprise Canyon, 4,000 ft, ♂, VII-5-1971, on flowers of *Melilotus albus* Desr. (J. W. Stubblefield, JWS). Narrows of Surprise Canyon, 3,600 ft, ♀, VIII-9-1971, on flowers of *Melilotus albus* Desr. (J. W. Stubblefield, JWS). Slaughterhouse Spring (in Panamint City), 6,400 ft, 2 ♂, VII-26-1971, on flowers of *Clematis ligusticifolia* (J. W. Stubblefield, JWS); ♂, VII-26-1971, on flowers of *Asclepias fascicularis* Dcne. in A. DC. (J. W. Stubblefield, JWS); ♂, VII-30-1971, on flowers of *Clematis ligusticifolia* (J. W. Stubblefield, UCD); ♀, VII-30-1971, on flowers of *Clematis ligusticifolia* (J. W. Stubblefield, JWS). Spring above Thompson Camp, Panamint Mts. (upper Surprise Canyon, actually Water Canyon), 6,800 ft, ♀, VII-22-1971 (J. W. Stubblefield, JWS). *San Diego Co.*: Julian, ♀, VII-4-1962 (J. H. Froebe, UCD).

UTAH: *Emery Co.*: Capitol Reef, E edge, ♀, IX-15-1979 (F. Parker and D. Veirs, BBSL). Goblin Valley State Reserve, 2 mi N, 5,000 ft, ♂, VIII-25-1982 (A. S. Menke, K. A. Menke, and F. D. Parker). Little Gilsen Butte, 5,000 to 5,100 ft, ♂, VIII-24 to 27-1980 (F. D. Parker and T. L. Griswold, BBSL); 2 mi E, 5,100 ft, ♂, ♀, VIII-24 to 26-1981 (Veirs, Griswold, and Parker, BBSL). Wild Horse Creek N of Goblin Valley, 4,900 ft, ♂, VII-23-1982 (Parker and Griswold, BBSL); ♀, 3 ♂, VII-25 to 28-1983 (Parker and Griswold, BBSL); 4,800 ft, ♂, ♀, VII-26 to 28-1982 (Parker and Griswold, BBSL). *San Juan Co.*: Rainbow Bridge National Monument, 3 ♂, VII-16-1935 (C. T. Brues, holotype No. 23397 and paratype, MCZ; paratype No. 55828, USNM).

Remarks: *Stizus iridis* is closely related to *S. occidentalis* but differs from that species in a number of details and can be immediately recognized by its much more extensive yellow coloration. The two species are ecologically quite distinct. In Inyo Co., California, where I have observed both species in the field, *S. iridis* is a summer species of desert mountain ranges, while *S. occidentalis* is a vernal species of the surrounding valleys. The two species are locally sympatric in the San Rafael Desert of Utah where they have been collected together in late July. Aside from this remarkably late record for *S. occidentalis*, collection dates for *S. occidentalis* range from March to June, while those for *S. iridis* range from July to September. The nesting biology of *S. occidentalis* remains unknown, but Dow (1976) has reported on two active nests of *S. iridis*. Both nests consisted of a sloping tunnel terminating in a single cell stocked with adult acridids of the genus *Trimerotropis*.

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The Spiny Orb-Weaver Genera *Micrathena* and *Chaetacis* (Araneae: Araneidae)

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THE SPINY ORB-WEAVER GENERA *MICRATHENA* AND *CHAETACIS* (ARANEAE: ARANEIDAE)

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ABSTRACT. *Micrathena* and *Chaetacis*, members of the subfamily Gasteracanthinae, share two specialized characters: fourth femora longer than first and book-lung covers with stridulatory ridges. Along with other gasteracanthine species, they have a sclerotized ring around the spinnerets and a paramedian apophysis in the palpus. Both genera are neotropical, with only few species of *Micrathena* extending their ranges into the nearctic region.

A function of the spines on the abdomen might be to disguise the spider's outline when resting in the web.

There are 104 species of *Micrathena* and nine species of *Chaetacis*. Twenty-nine species of *Micrathena* are new and four of *Chaetacis*: *M. glyptogonoides* from central and northern Mexico; *M. lenca, M. tziscao, M. petrunkevitchi,* and *M. margerita* from Chiapas, Mexico; *M. banksi* from Cuba; *M. gurupi* from Suriname; *M. kochalkai, M. atuncela, M. bogota, M. marta, M. anchicaya* from Colombia; *M. pilaton, M. balzapamba, M. guayas, M. pichincha* from Eucador; *M. huanuco, M. exlinae* from Peru; *M. ucayali, M. embira, M. coca* from the upper Amazon; *M. bananal, M. alvarengai* from Mato Grosso, Brazil; *M. reali, M. teresopolis, M. guanabara, M. jundiai, M. soaresi* from southeastern Brazil; and *M. coroico* from Bolivia; *Chaetacis osa* from Costa Rica; *C. carimagua* from Colombia and Venezuela; and *C. cucharas* and *C. woytkowskii* from Peru.

Ildibaha is a new subjective synonym of *Micrathena.*

Misplaced species are *Micrathena beta* di Caporiacco, a linyphiid; *M. conspicua* and *M. necopinata,* which are *Chaetacis*; and *Chaetacis rouxi,* a *Micrathena*. There are 93 new synonyms of *Micrathena* names, some uncertain because of difficulty in matching sexes and immatures with adults, others uncertain because of difficulty interpreting old Walckenaer's descriptions.

INTRODUCTION

The genus *Micrathena* contains many species of tropical, woodland orb-weavers which are diurnal in habits, spiny and often strikingly colored. Most species cannot readily be determined. They have been known for two hundred years; names and descriptions date back to Linnaeus. Among the earliest descriptions are those of Perty, with good accompanying illustrations. Perty's drawings, like those of Hahn and C. L. Koch, are readily recognizable depictions of *Micrathena* species. Confusion arose when Walckenaer based names on illustrations of his that were never published, and apparently are lost.[2] His inadequate, often contradictory descriptions are difficult to match with specimens. Despite Reimoser's (1917) studies and comparisons, and Chickering's five papers on the genus, *Micrathena* remained in a state of confusion.

My predecessors were hampered in their work: Reimoser's collections were small, and types of many names were not available to him. Thus, he accidentally gave new names to species described previously by Simon and Strand, authors who did not illustrate their new species. Chickering (1960–1964) failed to indicate how he separated the many related species. Even within the last fifty years additional species have been described and named from immature specimens that do not show diagnostic characters of adults; other descrip-

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[2] They could not be found in the Laboratory of Arachnids, Laboratory of Entomology, nor in the central Library of the Muséum National d'Histoire Naturelle, Paris, nor in the Library of the British Museum (Natural History).

tions lack the essential illustrations. Are these all distinct species or redescriptions of previously described ones?

One purpose of this revision was to see whether the very dimorphous males and females could be associated (Plates 1, 2). Of the 180 species of *Micrathena* listed in catalogs, only six were known from both females and males; 139 from females alone, 26 from males; and 3 from immatures (Roewer, 1942; Brignoli, 1983).[1] Only recently was Chickering (1960, 1961) able to match males and females of another four species.

Another question to be addressed concerns the function of the spectacular spines on the abdomen (Plates 1, 2): Do they provide a defense against predatory wasps, lizards or birds? More important, how does the genus fit into the evolutionary schema of the Araneoidea? Is their inability to attack-wrap prey, as do other orb-weaving spiders (Robinson, 1975; Eberhard, 1982), really a primitive character?

This is the first in a series of papers presenting revisions of tropical American orb-weavers of the families Araneidae, and Tetragnathidae.

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[1] While 12 are listed in catalogs as known from both sexes, six turned out to be mixtures or synonyms of other species known from both sexes (Roewer, 1942; Brignoli, 1983).

Plate 1. Upper row, left. Web of *Micrathena molesta*; orb about 8 cm diameter. Right. *M. schreibersi* in web. Middle row, left. *M. funebris*. Right. *M. furcula* with egg-sac. Bottom row. *M. sexspinosa*. Left. Female. Right. Male.

(Photo credits. upper left and middle row, right: J. Coddington; middle row, left: W. Maddison.)

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METHODS

Examination and Illustrations. Reflections make it difficult to examine the sculpturing of a dark structure with a stereoscopic dissecting microscope at fairly high power and under intense illumination. To avoid reflections, female *Micrathena* specimens were positioned on black silicon carbide (Carborundum®; Opell, 1983) in order to illustrate the epigynum and the dorsal and lateral views of the body. Later the specimens were transferred to a substrate of pale sand for drawing the profile of the epigynum and for measuring. Male palpi were illustrated while first on white paraffin with suitable depressions to observe the outline, then moved to black for studying the structure. Reflections could be further reduced by placing the palpus into a deep hole carved in the black paraffin. A Dolan-Jenner Fiber Lite (System 181-1) was used for illumination. This transmits a small but strong light beam from each of its two flexible arms; for illustrating, the right arm can be pushed aside to permit illumination from the upper left only.

The epigyna were placed in approximately the same positions to permit comparison. Palpi were illustrated in mesal view and showing the paracymbium in lateral view. In lateral view the palpi were positioned so that the tip of the conductor or median apophysis were barely visible, allowing easier repetition and comparison with others (Figs. 25, 497, 572).

Illustrations were made of the internal female genitalia of some species, but were discontinued when they were found to be of little aid in separating species, as they only supported characters found in the three-dimensional epigyna.

The drawings of epigyna are unorthodox in having the venter up in posterior view, and facing left in profile illustrations (Figs. 3–5). Had they been drawn conventionally (venter down, dorsum up), the body would have shadowed the light coming from the upper left. The epigynum was not removed from the specimen for illustration.

Measurements. Total length was measured from the clypeus to the midline at the end of the abdomen, between the posterior spines. Leg article measurements were made on the intact specimen in sand. Thus, figures are estimates to one tenth of a millimeter because of error in parallax, measuring different aspects of the article,

and because of measuring with a 400 square grid reticle eyepiece at low power. Measurements to one hundredth of a millimeter (as reported in many current revisions) would necessitate the amputation of legs and mounting on a slide for examination at high power to permit repetition of the same measurements.

Mapping. Finding collecting localities is always difficult because of poorly handwritten labels, misspellings, localities with similar names, and changes in locality names and spellings. To find names the following were used: gazetteers of the Geographic Society Index to Maps of Hispanic America, published 1944; the gazetteers of the U.S. Board of Geographic Names published by the U.S. Government for Latin American countries, 1954–1963. For nineteenth century Mexican and Central American localities, Selander and Vaurie (1962) is useful. Most imporant are the Ornithological Gazetteers currently published for South American countries and available from the Bird Department of the Museum of Comparative Zoology. The ornithological gazetteers give nineteenth century collecting sites of birds, many of which are the same for spiders.

Literature citations of lists of spiders found were not used, since experience has shown that many are misidentified. Only recently a list of spiders for a North American state was published, containing erroneous records and names long ago synonymized. While *Micrathena sagittata* appears on faunal lists of the West Indies, no specimens were found in collections; collections include only the similar *M. militaris*. It is an almost hopeless task to expunge such misidentifications from catalogs.

Associating Males with Females. The biggest problem in the genus is matching males and females (Plates 1, 2). The following assumptions and procedures were used:

The first step was to sort females into species groups and to associate each male with a species group. Females from tropical America were sorted into species groups using the form of the epigynum as the predominating character. When placing the four species occurring north of Mexico by this criterion, it was found that each belonged to a different group. It was assumed that males and females of the four well-known species from north of Mexico were correctly matched (Levi, 1978). This assumption provided information on the form of the palpus for the three groups containing most species. The fourth species group, the *funebris* group, contained only *M. funebris*. Next, it was assumed that the common *M. schreibersi* and *M. sexspinosa* had been matched correctly by Chickering, providing information on males of two additional species groups. Males not belonging to any of the above groups were then assumed to represent the *triangularispinosa* and *lepidoptera* groups. To match males of these last two groups proved most difficult and time consuming.

The next step was to match collecting sites of males and females of the same group. However, because several related species may have overlapping distributions, associating even those males and females collected together is not reliable. It is here that mistakes may have been made. Also, some commonly occurring males were eventually matched to commonly occurring females; some were matched by elimination, others because of similar color of the sternum. Any attempt at associating males with females is more likely to be correct if done within the framework of a revision rather than as a result of casual field collecting. Still, I hope that field work and observed matings will show whether my pairs are correct.

New Species. New species were named only if both the genitalia and the carapace or abdomen differed. It is often difficult to decide whether a single specimen with aberrant genitalia, unusual texture of the abdomen, or additional spines represents a new species or variability within one species.

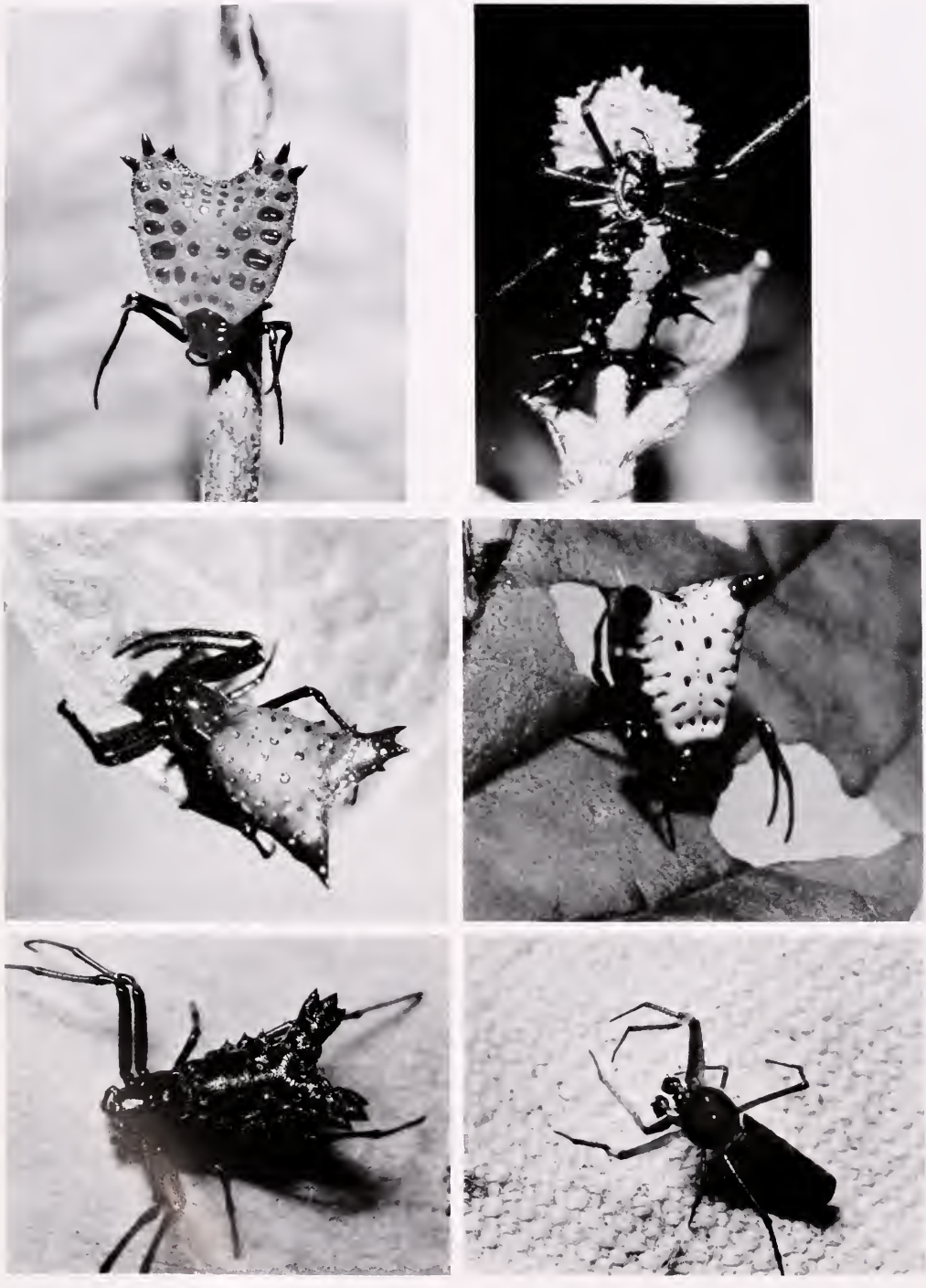


Plate 2. Upper row, left. *Micrathena clypeata*. Right. *M. lepidoptera*. Middle row, left. *M. molesta* with parasitic mite on right anterior of abdomen. Right. *M. saccata*. Bottom row. *M. triserrata*. Left. Female. Right. Male.

(Photo credits. Upper row, right: J. Coddington. Middle row, right: A. Aiello. Bottom row: W. Maddison.)

RELATIONSHIPS

Micrathena and *Chaetacis* have always been thought closely related, but their relationship to other araneids has been considered uncertain. Simon (1895) placed *Micrathena* in his large family Argiopidae (including Tetragnathidae and Linyphiidae), subfamily Argiopinae, group Micratheneae. F. P.-Cambridge (1904) divided the family into subfamilies: Theridiosomatinae, Linyphiinae, Tetragnathinae, Metinae, Nephilinae, Argiopinae, Araneinae, and Gasteracanthinae (including *Micrathena*). The first five are now considered families, the last three subfamilies. Dahl (1913) split the family, creating 12 subfamilies in the Araneidae, and separating Gasteracanthinae and Micratheneinae without explanation.

The synapomorphous characters which unite *Micrathena* and *Chaetacis* are:

1. *Micrathena* and *Chaetacis* have a stridulatory surface on the book-lung covers (absent, perhaps lost, in the *M. spinosa* and *M. militaris* species groups). This stridulating surface (Plate 3) is a synapomorphy of the two genera, a character not known from other orb-weavers except some erigonids (Hinton and Wilson, 1970). It is assumed that the presence of the structure in araneoid Erigonidae and araneoid Araneidae is parallel evolution and not a synapomorphy.

2. *Micrathena* and *Chaetacis* species have the fourth femora longer than the first, a synapomorphy not found in any other araneid genus. It permits the unique, cryptic resting position known from *Micrathena* (but assumed for *Chaetacis*; Plate 1).

3. In *Micrathena* and *Chaetacis* the carapace is glabrous, almost always lacking setae (except in *M. furcula*), with sculpturing and often a series of one to three pairs of dimples and a high thorax (Plates 1, 2). The *triangularispinosa* group has a glossy, domed carapace without dimples or grooves. Both the dimples and the often high or dome-shaped thorax are unique to these araneid genera and are a synapomorphy of the two genera. I consider carapace shape an important character to unite species, species groups, and genera in Araneidae. It has been underrated because of the difficulty in describing this part of the spider's anatomy.

4. In all species of *Micrathena* and *Chaetacis* the paracymbium is relatively large and modified (Figs. 8, 9). It is not in *Gasteracantha*; in most araneid genera (except perhaps in *Verrucosa*) it is just a knob. In males of the Metidae and Tetragnathidae it is a very large structure; this is a parallel development and not indicative of relationship.

Heimer (1982) and Heimer and Nentwig (1982) state that the function of the paracymbium is to stop the twist of the expanding palpus by butting against the median apophysis (first observed by Grasshoff, 1968), and that the median apophysis matches and fits the paracymbium. Although the paracymbium is large and modified in many *Micrathena* and *Chaetacis*, it does not closely fit and match the size or shape of the median apophysis. The median apophysis does, however, match and fit (to some extent) the scape of the female epigynum into which it hooks during mating (Grasshoff, 1968).

Micrathena, *Chaetacis* and *Gasteracantha* are placed in the subfamily Gasteracanthinae because of the sclerotized ring around the spinnerets. This ring is not otherwise found in araneids, except for the neotropical *Xylethrus* and *Enacrosoma*, whose placement is uncertain. It could be argued that the ring is a poor character, evolving in connection with a sclerotized abdomen. However, there is as yet no good evidence that *Xylethrus* and *Enacrosoma* have evolved the ring independently (they might also be gasteracanthines). Also, the remaining genera with a sclerotized abdomen, such as *Acanthepeira* and *Wagneriana*, lack the ring. *Micrathena* and *Gasteracantha* are also united by the lack of attack-wrapping, a behavior believed present in most Araneidae species. Since

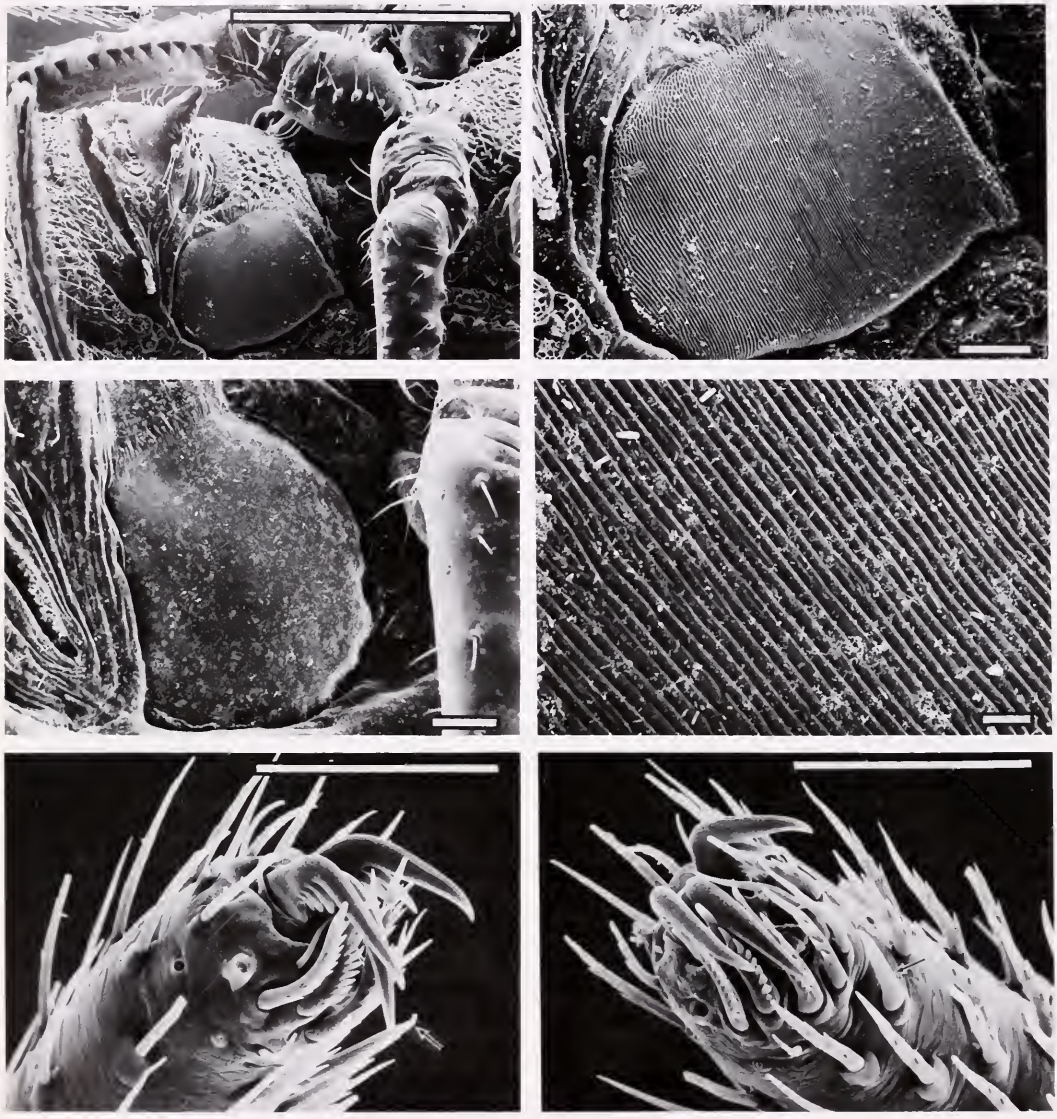


Plate 3. Upper row. *Chaetacis aureola*. Left. Epigynum, left book-lung, fourth coxae. Right. Left book-lung cover of *C. aureola*. Middle row, left. Book-lung cover of *Micrathena mitrata*. Right. Close-up. Bottom row. Tip of left fourth leg of *Micrathena mitrata* with sustentaculum (arrow).

Scale lines. Upper left 1.0 mm; right middle row 0.01 mm; others 0.1 mm.

this is a lost character it may be a poor one. Although the grouping of *Micrathena, Chaetacis* and *Gasteracantha* is supported at present, the support is not convincing. More characters are being sought.

According to Reimoser (1917), Gasteracanthinae lack a sustentaculum (Webestachel). The sustentaculum is a macroseta with a bent tip, located below the claws on the tip of the leg. It was found on *M. mitrata* (arrows, Plate 3); I suspect it is present in other species.

The relationship of Gasteracanthinae to other araneids is more problematic. The following characters were examined in an attempt to relate the Gasteracanthinae to other araneids.

1. *Paramedian Apophysis.* Many of the most useful structures indicating relationships are found in genitalia, especially in the complicated araneid palpus (see Levi, 1983). Characteristic of *Micrathena*, *Chaetacis*, and *Gasteracantha* is the relatively simple appearance of the contracted or expanded palpus (Figs. 6–9; Levi, 1978). But despite their apparent simplicity, both the *Micrathena* and *Gasteracantha* palpi have a paramedian apophysis (PM in Figs. 6, 7, 9), a sclerite not found in all male Araneidae. This structure, usually cap-shaped, was first described and named by Comstock (1910) in the palpus of *Eriophora*. Its function is not known. In *Eriophora* and other genera (Table 1), it is usually found near the proximal end of the conductor in the center of the mesal face of the palpus; it is fused to the conductor in *Verrucosa* (Levi, 1976: fig. 9) and in *Cyclosa* (Levi, 1977: fig. 17). It is a free sclerite in *Acanthepeira* (Levi, 1976: fig. 21), *Eriophora* (Levi, 1970: fig. 2), *Wagneriana* (Levi, 1976: fig. 71) and *Wixia* (Levi, 1976: fig. 99). It is absent in many araneids (Table 1; in *Eustala* the conductor has a projection that might be homologous). The absence of the paramedian apophysis is assumed to be the plesiomorph state and not a secondary loss (with some exceptions; see next paragraph). The paramedian apophysis is a prominent sclerite in *Gasteracantha* (Levi, 1978: fig. 84); in the *Micrathena mitrata* species group it is attached to the end of the conductor (Levi, 1978: fig. 40). It might be present as a lobe of the conductor in the *M. gracilis* group (Levi, 1978: fig. 68). It is absent in *M. funebris* (Levi, 1978: fig. 27), and absent in *M. sagittata* (Levi, 1978: fig. 54). Is the absence in some species of *Micrathena* a secondary loss? More weight is given to the unique long fourth femur and unusual web resting position, the unique carapace dimples, and the sclerotized ring around the spinnerets, characters which leave no doubt that all species groups of *Micrathena* are closely related. Gasteracanthinae thus forms a group of genera together with *Verrucosa*, *Acanthepeira*, *Cyclosa*, *Eriophora*, *Wagneriana*, and *Wixia* (and perhaps with other genera whose paramedian apophysis has been lost secondarily; see below).

2. *Terminal Apophysis.* The terminal apophysis is found in most araneid spiders. It is a sỳnapomorphy of a large group containing most araneids. Within this group the size and shape of the terminal apophysis may be useful, but at present its use as a character is uncertain. It is absent in *Argiope*, *Gea* (Levi, 1983), *Acanthepeira* (Levi, 1976: fig. 21), and *M. schreibersi* (Fig. 9). Its absence in *Argiope* and *Gea* is probably plesiomorph (Levi, 1983). The structure may have been lost in *Acanthepeira*, as a paramedian apophysis is present. It is lost in *M. schreibersi*; in other *Micrathena*, in *Chaetacis* and in *Gasteracantha* it is present as a mere flap covering the embolus (A in Figs. 6–8). In *Araniella*, *Acacesia* and *Neoscona* the terminal apophysis is small. The paramedian apophysis may have been secondarily lost in *Araniella* and *Acacesia* (probably not in *Neoscona*).

3. *Distal Hematodocha.* Males having a paramedian apophysis, which include *Micrathena*, *Chaetacis* and *Gasteracantha*, lack a distal hematodocha and have a small terminal apophysis. *Verrucosa* is an exception (Table 1). In most genera close to *Araneus* the distal hematodocha is present and is a synapomorphy of these genera (Table 1).

4. *Coxal Hook.* The first coxa of araneid males has a prominent hook at the distal margin, ventral in most genera. It fits into a groove at the proximal end of the second femur (Figs. 1, 2). Hook and groove are present in most species of *Araneus* (but not in all; Table 1). Coxal hook and groove are absent, perhaps secondarily lost, in *Acanthepeira*, *Hypsosinga*, *Kaira*, *Larin-*

TABLE 1. TABLE OF CHARACTERS OF MALE SPIDERS OF SOME ARANEID GENERA.

	ET	CX	CDY	PM	DH	TA	Species examined
Argiopinae	−	−	−	−	−	−	
Mecynogea	−	−	−	−	−	−	
Cyrtophora	−	−	−	−	−	−	
Pronous	+	+	−	−	−	−	
Hypsosinga	+/−	−	−	−	*	**	*rubens, pygmaea*
Kaira	−	−	−	−	**	*	*alba*
Larinia	+	−	−	−	**	**	*directa*
Araneus	+/−	+/−	+/−	−	**	**	
Aculepeira	+	+	+	−	**	**	*carbonaria, packardi*
Cercidia	+	+	−	−	**	**	*prominens*
Colphepeira	+	+	−	−	*	**	*catawba*
Eustala	+	+	+	−	*	**	*clavispina, fuscovittata*
Mangora	+	+	+	−	**	**	*gibberosa, placida*
Metazygia	+/−	+	+/−	−	**	**	*gregalis, wittfeldae*
Metepeira	+/−	−	−	−	**	**	*ventura, foxi*
Nuctenea	+	+	−	−	**	**	
Singa	−	+	−	−	**	**	*eugeni*
Scoloderus	−	+	−	−	−	*	*cordatus*
Araniella	+	+	+	−	−	*	*displicata*
Acacesia	+	+	+	−	−	*	*hamata*
Verrucosa	+	+	−	A	*	**	*arenata*
Cyclosa	+	+	−	A	−	*	*conica, turbinata*
Micrathena	−	+/−	−	F/A	−	*	
Chaetacis	−	−	−	F/A	−	*	all
Gasteracantha	−	−	−	F	−	*	*cancriformis*
Acanthepeira	+	−	−	F	−	−	*stellata*
Eriophora	+	+	+	F	−	**	*edax*
Wagneriana	+	+	+	F	−	**	*tauricornis*
Wixia	+	+	+	F	−	**	*ectypa*

Abbreviations:
ET endite tooth
CX coxal hook
CDY condyle on dorsum of coxa I
PM paramedian apophysis
DH distal hematodocha
TA terminal apophysis

Key:
(−) absent
(+) present
* small
** large
A attached
F free

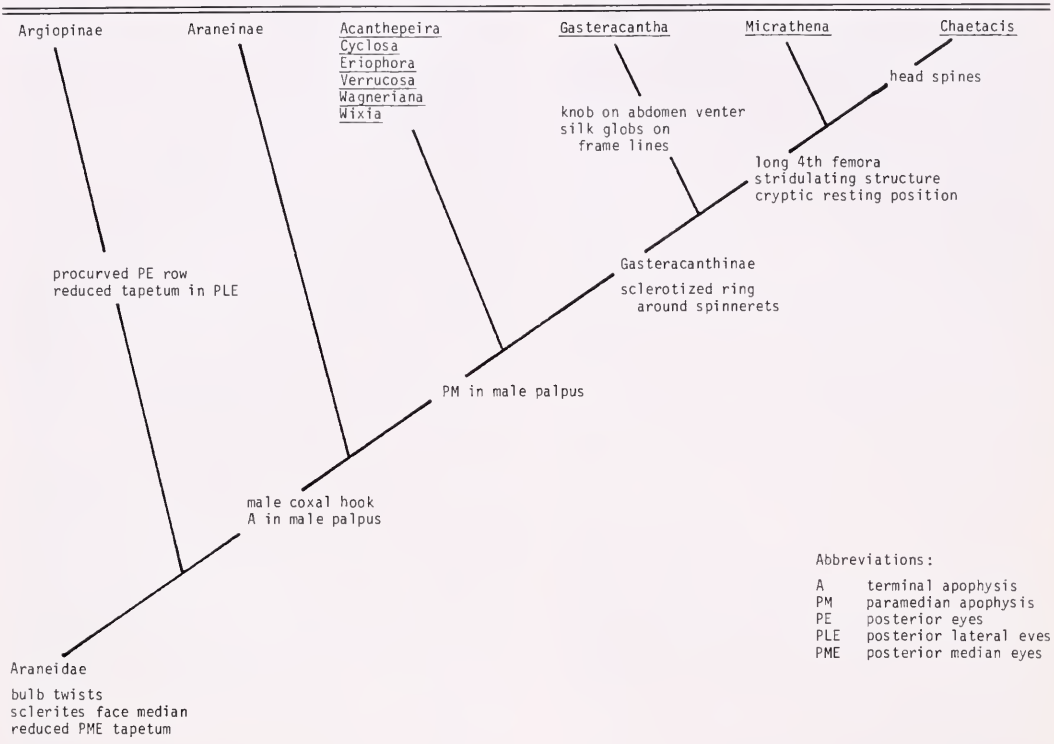
ia and *Metepeira* (Table 1). Both are also absent in *Argiope* and *Gea*, although here this is almost certainly a plesiomorph condition, as they are absent in all non-araneid Araneoidea.

This coxal hook is present in species of the *M. kirbyi* and *M. guerini* groups of *Micrathena* only; it is small and is more posterior on the coxa (Fig. 2). A matching groove on the second femur is present (Fig. 1). Only *M. clypeata* shows a prominent ventral hook. In other *Micrathena* species groups and in *Chaetacis* and *Gasteracantha*, the coxal hook is absent, assumed secondarily lost because the paramedian apophysis is present. In species belonging to the same group more weight is given to the presence of a structure than to its absence.

5. *Tooth on Endite. Micrathena* and *Chaetacis* males also lack a tooth on the lateral face of the endite facing a similar tooth on the palpal femur. This structure is present in most araneid genera examined (Table 1). It is absent, perhaps secondarily lost, in *Larinia*, *Scoloderus*, *Wagneriana* and probably absent primitively in *Argiope* and *Gea*. Its absence cannot be used to relate genera.

Summary of Relationships. Micrathena, Chaetacis and *Gasteracantha* belong together in the subfamily Gasteracanthi-

TABLE 2. TENTATIVE CLADOGRAM SHOWING POSITION OF SUBFAMILY GASTERACANTHINAE WITHIN THE FAMILY ARANEIDAE (SEE ALSO TABLE 1).



nae, a group of Araneidae with specialized characters. (The subfamily Argiopinae exhibits many primitive characters; Levi, 1983.) The inability to attack-wrap must therefore be a secondary loss and not the primitive condition (Tables 1, 2).

Unsolved Problems. Foremost among the numerous unresolved questions is whether the males of species have been correctly matched to females. Does the male with a *Chaetacis*-like palpus (Fig. 790) actually belong to *M. pungens*? Are the specimens assigned to *M. furva* in fact southern specimens of *M. digitata*? Why are females of the *M. agriliformis* group (including *M. fidelis* and *M. pupa*) relatively uncommon compared to males? Are they misidentified? Is the widespread *M. lucasi*, with its variable spines, really a single species? To answer this question it would be helpful to have more males collected with females. Do some highly variable *Micrathena* species hybridize, as is suggested by specimens in collections? This applies especially to *M. plana* and *M. triangularis, evansi* and *triangularispinosa*, and to variable *Chaetacis* species.

Gasteracanthinae O. P.-Cambridge

Gasteracanthides O. P.-Cambridge, 1871: 217. Name given to a new family. Bonnet, 1957: 1974.

Included in this subfamily are araneid genera, in which both males and females of the species have a sclerotized ring around the spinnerets.

There may be five or six gasteracanthine genera in America. *Gasteracantha* includes two species: *G. tetracantha* in Puerto Rico, and *G. cancriformis* from the southern United States to northern Argentina. The two species are not genetically

isolated in the Bahamas, and intergrade in appearance (Levi, 1978). *Micrathena* and *Chaetacis* are revised here.

Other American gasteracanthine genera may be *Enacrosoma* Mello-Leitão, *Xylethrus* Simon, and *Thaumastobella* Mello-Leitão. Practical considerations made me revise *Micrathena* and *Chaetacis* first: the species are readily recognized and sorted out from collections, and therefore available for borrowing. Behavior observations are available. *Enacrosoma* Mello-Leitão and the rare *Xylethrus* will be revised later. No specimens other than the lost type of *Thaumastobella mourei* Mello-Leitão have been found. We do not know whether or not members of these three genera attack-wrap, or whether the ring around the spinnerets is a synapomorphy for all genera.

Pronous Keyserling and *Tecmessa* O. P.–Cambridge have been placed in the subfamily (Roewer, 1942; Brignoli, 1983). Neither is a gasteracanthine. The placement of *Pronous* is uncertain (Table 1); *Tecmessa* is a theridiosomatid (Coddington, in press).

Numerous gasteracanthine genera are known from Africa; some had been synonyms of *Gasteracantha* but were resurrected by Benoit (1962).

Micrathena Sundevall

Micrathena Sundevall, 1833: 14. Read in April 1833 (F. P.-Cambridge, 1904: 525); publication date unknown. Type species *Epeira clypeata* Walckenaer, the only species listed in section one of the genus, designated by Simon, 1895.

Acrosoma Perty, 1833: 193. Published in December 1833 (F. P.-Cambridge, 1904: 525). Type species *A. swainsoni* Perty designated by F. P.-Cambridge 1904: 525. Bonnet, 1955 curiously cites two type species: *Aranea cancriformis* Linnaeus, the oldest species included by Perty, and *M. militaris* Perty, the first species cited by Perty (see below).

Meganopla Simon, 1864: 292. Type species *M. cyanospina* (Lucas) designated by Bonnet, 1957: 2752.

Keyserlingia O. P.-Cambridge, 1890. Type species by monotypy *K. cornigera* O. P.-Cambridge (=*M. sexspinosa*). The name *Keyserlingia* is preoccupied by Pander, 1861 for a Brachiopod.

Ildibaha Keyserling, 1892: 31. Type species *I. albomaculata* (=*M. flaveola*) Keyserling by monotypy. NEW SYNONYMY.

Synonymy. Of the two oldest names, both proposed in 1833, *Micrathena* has priority. Bonnet (1957) claims that, since Sundevall was the only author to distinguish between *Micrathena* and *Gasteracantha*, one has to use Sundevall's name *Micrathena*. However, it is the type designation for the genus which determines its use, not the species included. Because types were often casually designated by later authors, the type designation is frequently difficult to ascertain. Roewer, in the first volume of his catalog (1942) fails to give a type for genera; Bonnet's catalog often gives a different type designation from that found in the literature (also for *Acrosoma*), and does not say who designated the type species.

The type of *Micrathena, M. clypeata,* belongs to the *kirbyi* group; that of *Acrosoma, M. swainsoni,* belongs to the *militaris* group, as does the type of *Meganopla, M. cyanospina.* The type of *Keyserlingia* belongs to the *spinosa* group, and the type of *Ildibaha, I. albomaculata,* to the *M. triangularispinosa* group of species.

Diagnosis. Micrathena and *Chaetacis* differ from other gasteracanthine genera by having the fourth femur longer than the first (in females and males). *Micrathena* differs from *Chaetacis* by lacking spines or tubercles on the carapace behind the lateral eyes. Both differ from *Gasteracantha* by the differently shaped carapace: *Gasteracantha* has the anterior head region very high (Levi, 1978: figs. 70, 71), while *Micrathena* and *Chaetacis* do not. *Chaetacis* has tubercles or spines behind the lateral eyes and often has denticles on the carapace. Unique to *Micrathena* are the high thorax, low head, and the glabrous, sculptured carapace with a deep thoracic depression (Figs. 89, 90), often with one to three pairs of dimples (Figs. 74, 75). Larger species have a light colored rim on each side of the thorax; in smaller species the rim can be seen only from the side. Only the *triangularispinosa* group of species has the carapace different: domed and smooth, often shiny,

with at most a faint depression in the area of the thoracic depression (Figs. 432, 433).

Other characters unique to *Chaetacis* and *Micrathena* are the stridulating ridges on the book-lung covers (Plate 3), the pick being a tubercle on the fourth femur. However, members of the *M. militaris* and *M. spinosa* groups lack these structures, perhaps a secondary loss.

Description. The posterior median eyes are subequal to two diameters of the anterior medians. The laterals are usually smaller, the posterior laterals usually smallest. Anterior median eyes are their diameter apart, posterior median eyes about their diameter apart. Lateral eyes touch, except in the *militaris* and *spinosa* groups, which may have the eyes as much as one diameter apart. The tapetum of the posterior median eyes is reduced to a narrow section, characteristic of the family Araneidae (Levi, 1978: figs. 19, 32).

The abdomen of *Micrathena* females bears large spines, sometimes tubercles or humps; as in other members of the Gasteracanthinae, there is a sclerotized ring around the spinnerets. The dorsum is often shiny and brightly colored: white, yellow, orange to brown; the venter is usually gray to brown (Plates 1, 2).

The male never has a tooth on the endite, nor a tooth on the palpal femur. Half the species have a coxal hook (Fig. 2) and a groove on the proximal end of the second femur (Fig. 1). Both tooth and groove are relatively small (compared to the structures in other genera) and the coxal hook has moved retrolaterally (except in *M. clypeata*, where it is ventral). In half the species both coxal hook and femoral groove are absent, apparently secondarily lost. Males often have the first two pairs of legs slightly heavier and with macrosetae, but not otherwise modified.

The abdomen of *Micrathena* males lacks spines (except *M. swainsoni* and *M. donaldi*) and is square to rectangular, longer than wide, very unlike that of the female associated with it. The abdomen of males of the *M. schreibersi* group has a constriction (Fig. 570). Males may be only slightly smaller than females (*guerini* group), or may be much smaller (e.g., *gracilis* group).

Genitalia. Females of *Micrathena* may have a wrinkled scape on the epigynum (Figs. 50, 55, 68), a primitive character. The epigynum has evolved into a raised transverse bar bearing a posteromedian lobe, both situated on a bulge that is delimited anteriorly by a transverse groove (Fig. 3); in profile the structure looks like a bird's head (Fig. 5). While half the species have a transverse bar with a lobe, others have only a sculptured bulge, with the sculpturing mainly on the posterior face (*triangularispinosa* group, Figs. 428, 434; *militaris* and *spinosa* groups, Figs. 584, 591, 648, 656). In all members of the *gracilis* group the bulge is pulled out ventrally, laterally flattened, and indented (Figs. 778–780).

The palpus has a conductor (C), almost always a large median apophysis (M) (lost in *M. flaveola* and *M. acutoides*), a radix (R), an embolus (E), and a small terminal apophysis (A) paralleling or surrounding the embolus (Figs. 6–9). The terminal apophysis is lost in the *M. schreibersi* group (Fig. 9). There is abundant basal hematodocha but no distal hematodocha, just a joint between radix and terminal apophysis-embolus. The proximal end of the conductor is drawn out into a paramedian apophysis (PM), which is usually cap-shaped and remains attached to the conductor (Figs. 6–9). As in metids, but unlike most other genera of the Araneidae, the paracymbium (P) is well developed; in some groups it is different in each species (Figs. 6–9).

Natural History. All *Micrathena* are forest species that hang in the vertical web during the day. *Micrathena* builds in the morning. The web is tight, with few frame threads and an open hub (Plate 1). It may have a short, vertical silk stabilimentum (*M. sexspinosa*). The spiders have an unusual resting position: the spider hangs head down in the center of the web with abdomen horizontal, parallel to the ground. This position is made possible by

the unusually long fourth femora (Plate 1). The often bright dorsal coloration of the abdomen faces the ground, effectively camouflaging the spider against the light blotches of the canopy. The dull underside faces upward and blends with the background vegetation and ground litter, making the spider equally hard to discern from above. The spines disrupt the spider's outline, preventing easy detection. The variable silhouette of different species adds to the difficulty of finding *Micrathena* species, as collectors cannot readily form a search image for a species. No species is very common in any locality, and different species, with different outlines and coloration, occur together. Furthermore, immatures often have different spination from adults.

Is the function of the spines to hamper the formation of a search image? Experiments might be devised to see if this is a defense against natural predators such as wasps, dragonflies, birds, or lizards. The long spines of *M. cyanospina* (Fig. 621) may be a direct protection against being carried off by predators. Also, it is known that some species of wasps will collect a specific *Micrathena* (but will not mix species, as they do with other genera). Large collections of the following were obtained from wasp cells: *M. mitrata*, *M. furcula*, *M. sexspinosa*, and *M. swainsoni*.

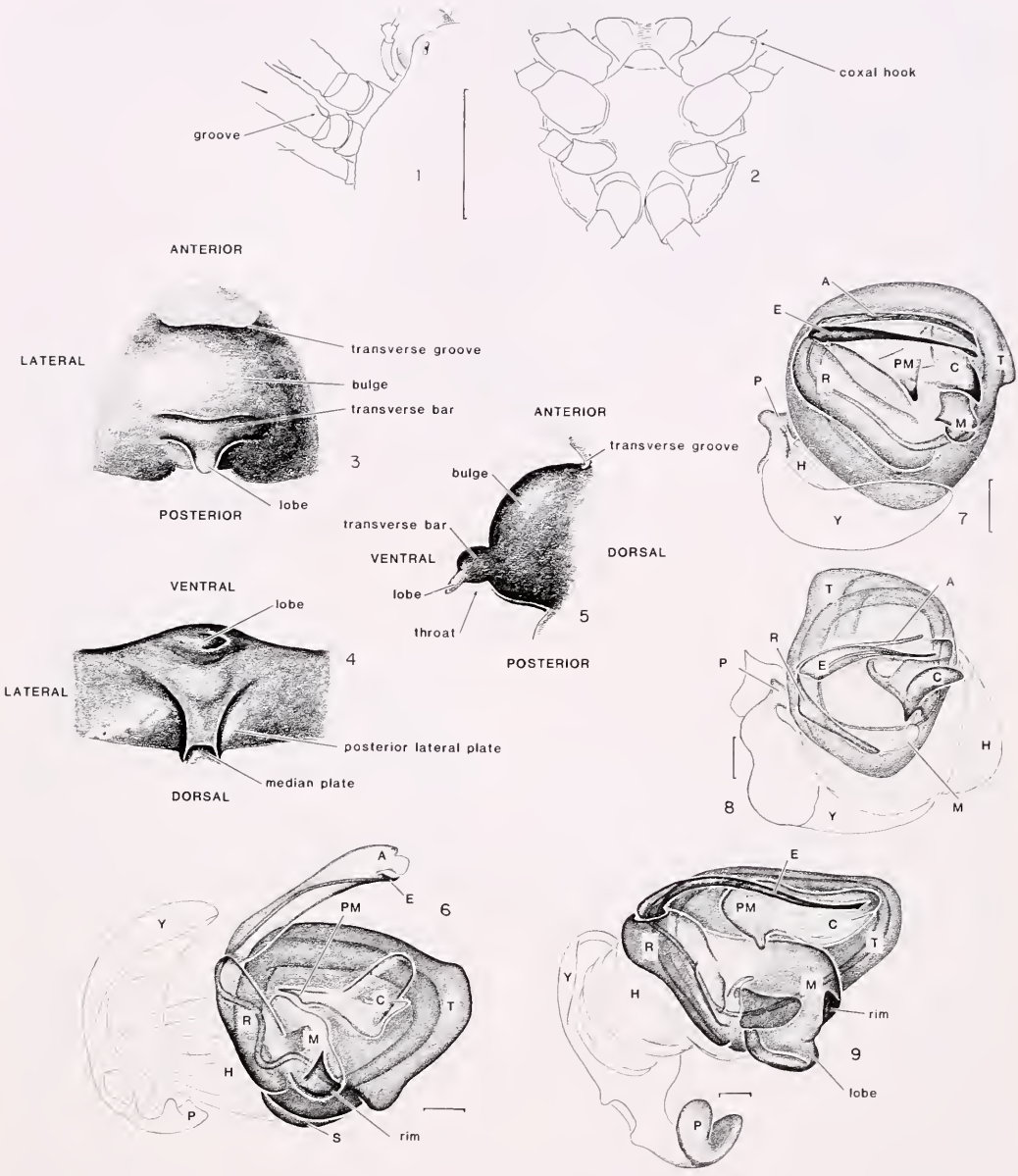
Micrathena gracilis and *M. horrida* have humps rather than spines (Figs. 774, 776, 777), and are gray to brown in color, rendering the spider invisible among the debris caught in the web. Robinson and Robinson (1980) call *M. horrida* a detritus mimic. Some specimens of *Micrathena funebris*, a variable species, have the black abdomen with orange spots framed by white (Plate 1; Fig. 734), a pattern found in juveniles of the venomous widow spiders (*Latrodectus* sp.). *Micrathena swainsoni* has been collected with similarly colored ants.

Micrathena do not attack-wrap (Robinson, 1975; Eberhard, 1982). Unlike other araneids, they bite their prey first, then wrap. Do the long fourth femora that facilitate the spider's cryptic resting position perhaps impede the extraction of wrapping silk? Probably not: the related *Gasteracantha*, with shorter fourth legs, does not attack-wrap either.

Uetz and Biere (1980) showed that the web of *M. gracilis* is selective for prey size: larger prey (4 to 8 mm) is caught than in artificial webs: Diptera comprise 66% of the catch, Hymenoptera 18%, and Coleoptera 10%.

Males are rarely collected with females. They are more likely to be picked up sweeping, often at night, while females are usually picked from their webs in daytime. It is uncommon to find males in the webs of females. Also, it is extremely uncommon to find mated males of species in which palpal structures break off and remain in the female epigynum (*M. spinosa* group). Is mating brief? Does it take place outside the web? Do males serve as food for the mated females? Robinson and Robinson (1980) have watched courtship and mating of *M. schreibersi* and *M. sexspinosa*. They state that *Micrathena* has type C courtship: copulation is brief and carried out on a mating thread. *Micrathena sexspinosa* males convert a radius from the upper part of the female's web into a mating thread. In each of the five observations the male was loosely wrapped by the female, allowing him to escape. Adult males taken to the laboratory died soon after collecting, indicating a short adult life span. It was also found that the constricted abdomen of *M. schreibersi* males (Figs. 570) permits them to "bend" when mating (Robinson and Robinson, 1980).

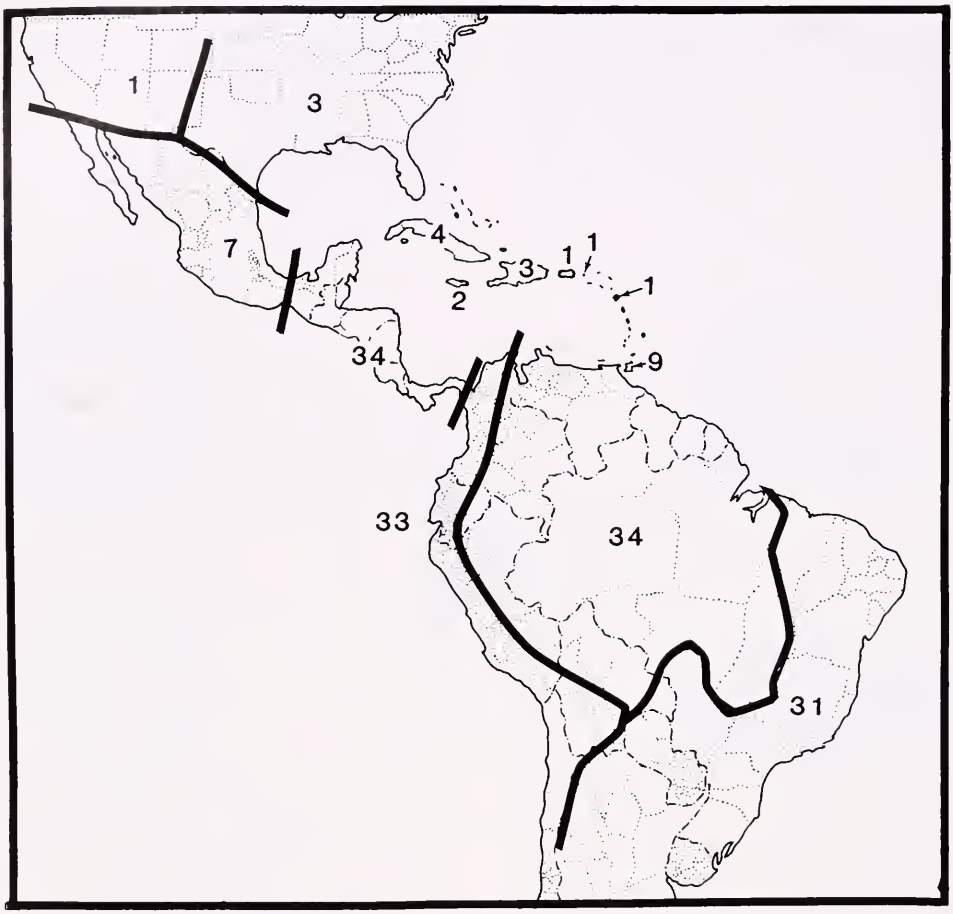
In this study it was found that in *M. schenkeli* and *M. molesta* as well as some other species (*M. raimondi*, *M. teresopolis*, *M. shealsi*, *M. bogota*), the lobe and sometimes the transverse bar of the female epigynum tears off during mating, presumably preventing later matings (Figs. 396–401, 482–486). In *M. militaris* and most species of the *spinosa* group, the



Figures 1–9. *Micrathena* morphology. 1, 2. Males. 1. Dorsal view of left side of head, proximal articles of palpus and first three legs, showing groove on second femur. 2. Ventral view of sternum, endites and coxae, showing coxal hook on first coxa. 3–5. Female epigynum. 3. Ventral. 4. Posterior. 5. Lateral. 6–9. Male left palpus, expanded. 1, 2, 6. *M. nigrichelis*. 7. *M. evansi*. 8. *M. flaveola*. 9. *M. schreibersi*.

Scale lines. 0.1 mm, except Figures 1, 2, 1.0 mm.

Abbreviations. A, terminal apophysis; C, conductor; E, embolus; H, basal hematodocha; M, median apophysis; P, paracymbium; R, radix; S, subtegulum; T, tegulum; Y, cymbium.



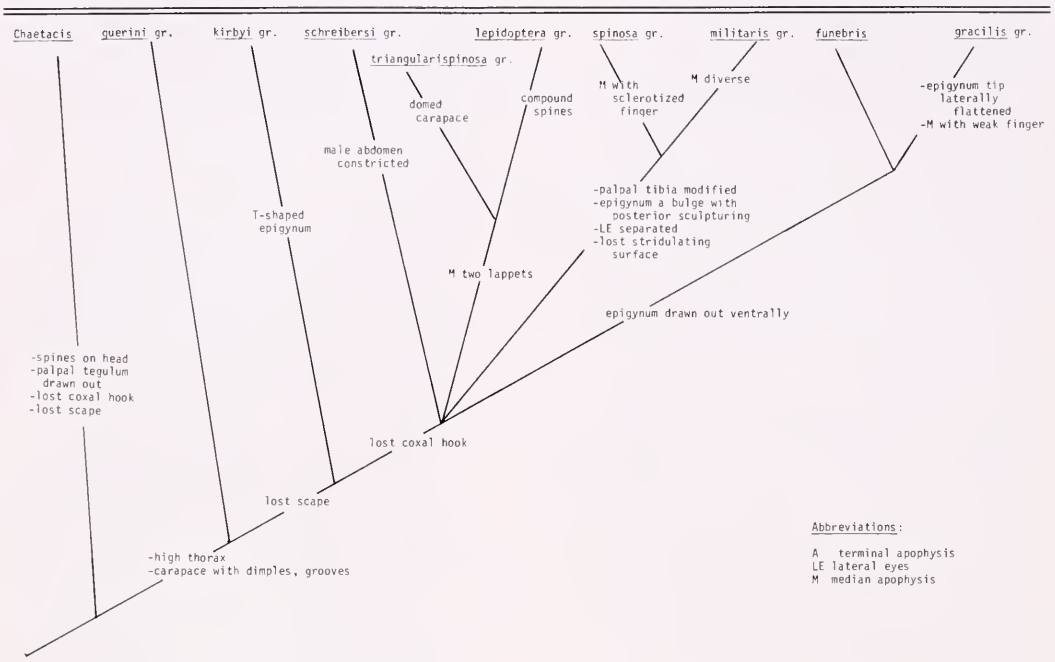
Map 1. The number of species of *Micrathena* in different areas.

embolus and terminal apophysis of the male palpus break off and plug the epigynum (Figs. 605–607, 729–731), making futher matings impossible for males and difficult for females.

Females place eggs in a fluffy egg-sac on vegetation near the web. Further knowledge is limited and comes from photographs (Plate 1). Young *Micrathena* look quite different from adults collected with them, and juveniles described as new species are exceedingly difficult to match with adult females. Juvenile males differentiate from females gradually, over the course of several instars. It would be instructive to raise young of different species groups from egg-sacs. Most species of the *Micrathena spinosa* group have an additional pair of spines as juveniles (Fig. 721); *Micrathena quadriserrata* immatures have fewer spines than do adults.

Micrathena and *Chaetacis* species have stridulating files on their book-lung covers (Plate 3) and pick on the fourth femora, and can produce an audible, low pitched buzz (Hinton and Wilson, 1970). The book-lungs act as a sounding board. These stridulating areas are present also in males, but could not be found in species belonging to the *M. spinosa* or *M. militaris* groups. The sound is probably a defense, as the spiders buzz when removed from

TABLE 3. CLADOGRAM OF SPECIES GROUPS OF MICRATHENA (*MICRATHENA PUNGENS* IS NOT INCLUDED).



the web. I have been unable to hear the sound, despite testing females of several species.

Distribution. Micrathena is a neotropical genus. Three species range to the eastern United States, one to the western states, seven to Mexico north of the Isthmus of Tehuantepec. There are 34 species in Central America south of the Isthmus; about 33 in the Andes and westward; about 34 in Venezuela and the Amazon basin; and 31 in southeastern South America (Map 1). In the Caribbean, two species occur in Jamaica, three in Hispaniola, four in Cuba, and nine in Trinidad; only one species at most occurs on the smaller islands of the West Indies (Map 1).

Different species are found at different elevations. For example, *M. fidelis*, *M. pupa*, and *M. agriliformis* are found in mountains; other species such as *M. clypeata* and *M. schreibersi* are found in lowland forests.

Micrathena are absent from the tropics of other continents, where numerous species of the related *Gasteracantha* may ocupy the same niche. While there are many species of *Gasteracantha* in other parts of the world, only two are found in the Neotropics (Levi, 1978).

Species Problems. Many *Micrathena* species were found to be variable, yet most are reasonably easy to distinguish, unlike the Old World *Gasteracantha* species. *Gasteracantha* species are known to be perplexingly variable and difficult to determine; they may hybridize (Chrysanthus, 1959; Emerit, 1974).

Genitalia are critical for separating species of the *Micrathena guerini*, *kirbyi* and *spinosa* groups. In some species groups (e.g., *schreibersi*, *militaris*, and *gracilis* groups) the shape of abdomen and carapace is often also diagnostic. Some species have so distinct an abdomen that immatures can be determined, but in many species immatures may have more (*spinosa* group) or fewer spines than adults (some species of the *kirbyi* group).

Relationships of Groups. The possible

relationships of the groups of species are shown in Table 3.

Misplaced Species

The following species had been misplaced.

Acrosoma aureolum C. L. Koch, 1836: 60, is a *Chaetacis*.

Acrosoma affinis C. L. Koch, 1839: 131, is *Chaetacis aureola* (C. L. Koch).

Acrosoma cornuta Taczanowski, 1873: 268, is a *Chaetacis*.

Acrosoma pictum C. L. Koch, 1836: 61, is a *Chaetacis*.

Acrosoma transitorium C. L. Koch, 1839: 119, fig. 518 is a *Wagneriana*.

Acrosoma tumida Taczanowski, 1879: 120, pl. 1, fig. 34, ♀ from Paltaypamba, Peru (PAN), examined = *Wagneriana undecimtuberculata* (Keyserling, 1864). NEW SYNONYMY. This name had been listed in Roewer (1942: 854) in *Aranea*, and in Bonnet (1955: 1948) in *Araneus*.

Micrathena beta di Caporiacco, 1947: 26; 1948, fig. 81, ♂ from Guyana is an adult male linyphiid, genus unknown. NEW FAMILY PLACEMENT.

Micrathena conspicua Mello-Leitão, 1929, is *Chaetacis picta* (C. L. Koch).

Micrathena necopinata Chickering, 1960c, is a *Chaetacis*.

Doubtful Names

Most of the doubtful names are Walckenaer's. His collection is lost, and thus not available for species verification. His descriptions refer to a manuscript of *Plectana* illustrations which was never published and is lost. I have synonymized names where the descriptions fit the species. The following remains:

Plectana bisicata Walckenaer, 1841: 194. This has ten split spines and a total length of 9 mm. It comes from South America. The description is unintelligible.

Other doubtful names are those of Mello-Leitão. This author often did not provide illustrations. Although most of his types are purported to be in the Museu Nacional, Rio de Janeiro, only few can be found there. The types deposited in other institutions were examined.

Micrathena mastonota Mello-Leitão, 1950. Female 7.5 mm total length from Est. Espírito Santo, Brazil (no. 58 345, MNRJ), lost. The carapace is low, flat, granulate, and has a small thoracic depression. The abdomen is highest at the spinnerets and has two anterior spines, six more on each side in two groups. The sides have four rounded tubercles, the posterior face a spine on each side, for a total of 16 spines. Perhaps this is *M. triangularis*?

Key to *Micrathena* Species Group

Females

1. Carapace evenly domed, often smooth and shiny, thoracic depression absent or an indistinct dent (Figs. 432, 433, 440, 441, 456, 457, 480, 481) ..... *triangularispinosa* group; p. 528
– Carapace with distinct circular thoracic mark, usually not shiny, often with dimples (Figs. 26, 27, 136, 137, 525, 526) 2

2(1) Epigynum drawn out ventrally into a cone, with cone tip laterally indented (Figs. 743–745, 758–760, 778–780) ..... *gracilis* group; p. 588
– Epigynum otherwise 3

3(2) Epigynum with a raised transverse bar on the bulge, usually with a posterior median lobe (Figs. 3–5), rarely V-shaped (Figs. 96, 151), triangular (Figs. 104, 112, 361, 378), profile usually bird's head-shaped (Fig. 5) ..... *kirbyi* group (in part); p. 460
– Epigynum otherwise 4

4(3) Abdomen with two lateral spines compound and posterior spines tripartite as in Figures 526, 535 ..... *lepidoptera* group; p. 546
– Spines on abdomen simple 5

5(4) Epigynum with a scape (Figs. 28, 30, 50, 55, 63, 68) or anterior lobe (Figs. 12, 20, 33, 42), sometimes torn off (Figs. 76, 86) and abdomen with 4 or 6 spines, or 8 small spines, none anterior (Figs. 27, 49, 75, 80, 85) ..... *guerini* group; p. 447
– Epigynum without scape or lobe; or, if with lobe, then abdomen with anteriorly directed spines overhanging carapace 6

6(5) Epigynum with a ventrally drawn-out bulge, often with light patch on anterior (Figs. 735–737) and abdomen with two to six fleshy spines (Figs. 732–734); U.S., to Central America, Map 12 ..... *funebris*; p. 586
– Epigynum and abdomen otherwise 7

7(6) Epigynum with projecting bulge, drawn out posteriorly, and two black openings on the posterior face (Figs. 786–788); abdomen with two large spines behind, one anterior pair and three lateral pairs (Figs. 784, 785); Venezuela, Amazon, Map 14 ..... *pungens*; p. 598

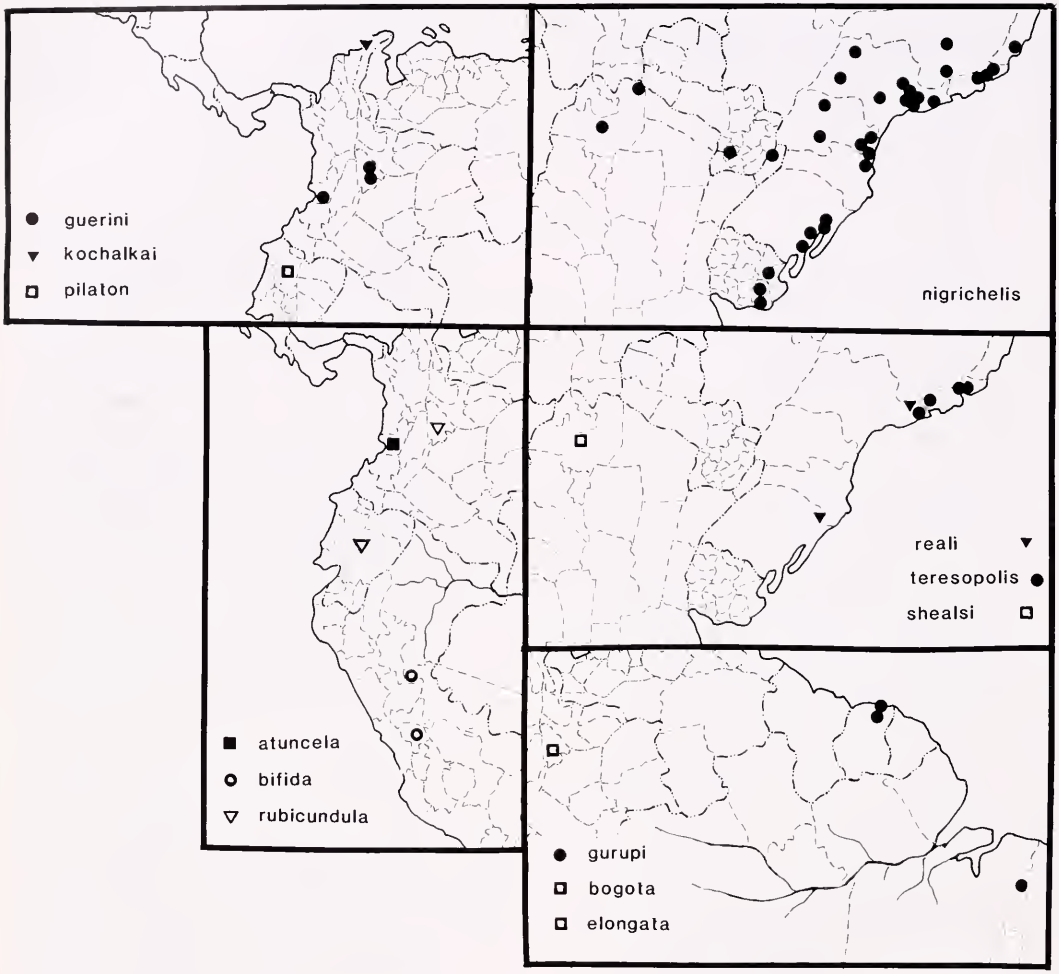
– Epigynum and abdomen otherwise 8
8(7) Length of abdomen more than twice width, slightly constricted on posterior half (Figs. 544, 639); southeastern Brazil to northern Argentina 9
– Shape of abdomen otherwise 10
9(8) Abdomen with ten humps tipped by spines (Figs. 543, 544); epigynal bulge with a pair of dents anteriorly (Fig. 545) ..... *spitzi*; p. 550
– Abdomen with eight sharp spines (Figs. 638, 639); epigynal bulge evenly curved anteriorly (Fig. 640) ..... *swainsoni*; p. 571
10(8) Abdomen without anterior spines, posteriorly biforked, with two to three pairs of dorsal spines (Figs. 646, 647, 654, 655, 683, 684, 712, 713) ..... *spinosa* group; p. 572
– Abdomen with anterior spines (Figs. 552, 557, 633, 634) 11
11(10) Abdomen biforked, forks bent upward; three pairs of small lateral spines and two pairs posterior (Figs. 551, 552); epigynum bulge crowned by a lobe (Figs. 553–555); Upper Amazon, Map 9 ..... *embira*; p. 552
– Abdomen and epigynum otherwise 12
12(11) Abdomen flat with a thick spine on each side, six behind (Fig. 419) or with lobes or small spines on sides, double or trifid spines on each side behind (Figs. 395, 406, 411) ..... *kirbyi* group (in part); p. 460
– Abdomen otherwise, with large spines (Figs. 557, 583, 621, 626) 13
13(12) Abdomen longer than wide, with a pair of white spines overhanging carapace and four pairs of large spines, third pair largest (Figs. 556, 557, 564, 565, 573, 574) ..... *schreibersi* group; p. 550
– Abdomen as long as wide, or wider than long, with pair of spines overhanging carapace and at most three additional pairs of spines (Figs. 583, 590, 598, 621, 626, 634) ..... *militaris* group; p. 558

Males

1. Abdomen constricted, suspected ant mimic (Figs. 548, 570, 579) ..... *schreibersi* group; p. 550
– Abdomen without constriction 2
2(1) First coxa with hook on distal margin (Fig. 2) fitting into groove on proximal end of second femur (Fig. 1) ..... *guerini* and *kirbyi* groups (in part); p. 447, 460
– First coxa without hook, second femur without groove 3
3(2) Carapace evenly domed; thoracic depression absent or at most a slight dent, usually smooth and shiny (Figs. 437, 477, 503) ..... *triangularispinosa* group; p. 528
– Carapace with distinct round thoracic mark, usually not shiny 4
4(3) Tegulum with tube-shaped ventral projection (Figs. 790, 791); Amazon, Map 14 ..... suspected male of *pungens*
– Tegulum never with such a projection 5
5(4) Distal margin of palpal tibia modified with lobe or lobes or ridges (Figs. 587, 595, 603, 631, 644, 652); without stridulating grooves on book-lung covers 6
– Distal margin of palpal tibia never modified (Figs. 540, 739, 768); with stridulating grooves on book-lung covers (Plate 3) 7
6(5) Median apophysis with a more or less sclerotized finger (Figs. 652, 660, 673, 710, 718) ..... *spinosa* group; p. 572
– Median apophysis never with finger (Figs. 595, 603, 614) ..... *militaris* group; p. 558
7(5) Median apophysis a sclerotized, curved spine (clockwise in left palpus), its base bearing a second spine (Fig. 739); paracymbium a flat corniculate plate (Fig. 740); U.S. to Central America, Map 12 ..... *funebris*; p. 586
– Median apophysis and paracymbium otherwise 8
8(7) Median apophysis lightly sclerotized, bearing a lightly sclerotized finger (Figs. 768, 772, 782) ..... *gracilis* group; p. 588
– Median apophysis never with finger 9
9(8) Median apophysis consisting of two lobes as in Figures 531, 532, 540, 541 ..... *lepidoptera* group; p. 546
– Median apophysis consisting of a squarish sclerite with its distal edge bent over and heavily sclerotized (males associated with females of *M. excavata*, Fig. 353 and *M. quadriserrata*, Fig. 375) ..... *kirbyi* group (in part); p. 460

The *guerini* Group

The *guerini* group is characterized by the female's lack of spines on the anterior of the abdomen, and by the presence of four large posterior spines (Figs. 11, 27) or, sometimes, six smaller spines (Figs. 85, 90). In addition, some species have a pair of spines on the sides (Figs. 54, 90). The epigynum has an anterior lobe or a scape (Figs. 12, 42, 68) which in some species is torn off when mating (Figs. 34, 76, 86). The carapace always has a distinct tho-



Map 2. Distribution of *Micrathena* species of the *guerini* group.

racic depression; some species have pairs of dimples (Fig. 75).

Males always have a hook on the first coxa (Fig. 2) fitting into a groove on the dorsum of the proximal end of the second femur (Fig. 1). The coxal hook is found also in males of the *kirbyi* group but not in others. The palpus is more diverse than in members of the *kirbyi* group. The cymbium may have a hump near its base above the paracymbium (Figs. 16, 17, 39, 47). The terminal apophysis is often sclerotized (Figs. 16, 38, 46); in *M. nigrichelis* it is a flat flap covering the embolus (Fig. 59); in *M. pilaton* it is absent (or perhaps torn off in the available specimens, Fig. 24). Also, the median apophysis and paracymbium show greater diversity (Figs. 46, 47, 59, 72) in structure than in members of the *kirbyi* group.

Diagnostic features of species are the arrangement of spines on the female abdomen, the shape of the scape or lobe and the surrounding area of the epigynum, and the shape of the embolus and terminal apophysis in the palpus.

The key to males is with the males of the *kirbyi* group, p. 467.

KEY TO THE *GUERINI* GROUP

Females

1. Abdomen with 8 small subequal spines, one pair on sides, three pairs posteriorly (Figs. 85, 90); Colombia 2
– Abdomen otherwise (Figs. 11, 41, 80) 3
2(1) Posterior median piece of epigynum wide ventrally close to scape (Fig. 87) ..... *bogota*
– Posterior median piece of epigynum narrow ventrally close to scape (Fig. 92) ..... *elongata*
3(1) Abdomen with 6 spines, two pairs posteriorly, one pair on sides (Figs. 41, 54, 80) 4
– Abdomen with 4 large spines, two pairs posteriorly, none or small denticles on sides (Figs. 11, 19, 27) 11
4(3) Eastern and southeastern South America: Brazil, Paraguay to Argentina 7
– Northwestern South America: Colombia to Peru 5
5(4) Epigynum with a scape (Fig. 50); Colombia, Ecuador, Map 2 ..... *rubicundula*
– Epigynum with a lobe (Figs. 33, 42) 6
6(5) Lobe of epigynum rounded (Fig. 42) and projecting ventrally (Fig. 44); Peru, Map 2 ..... *bifida*
– Lobe of epigynum with concave lateral margins (Fig. 33), curved posteriorly (Fig. 36); sometimes torn off (Fig. 34); Colombia, Map 2 ..... *atuncela*
7(4) Posterodorsal spines (second pair) larger than posterior spines (third pair) (Figs. 61, 66, 79) 9
– Second and third pair of spines subequal (Figs. 53, 74) 8
8(7) Sternum and venter of abdomen dark; scape of epigynum round (Fig. 55); Rio de Janeiro to northern Argentina, Map 2 ..... *nigrichelis*
– Sternum and venter of abdomen light; scape frequently torn off (Fig. 76); northern Argentina, Map 2 ..... *shealsi*
9(7) Scape of epigynum smooth and diamond-shaped (Fig. 81); Suriname, Est. Pará, Brazil, Map 2 ..... *gurupi*
– Scape wrinkled (Figs. 63, 68); southern and southeastern Brazil 10
10(9) Scape of epigynum with distal neck in ventral view (Fig. 68) and with a dewlap (Fig. 70); southern Brazil, Map 2 ..... *reali*
– Scape of epigynum without neck (Fig. 63); without dewlap (Fig. 65); Est. Rio de Janeiro, Brazil, Map 2 ..... *teresopolis*
11(3) Dorsal pair of abdominal spines longer than ventral pair (Figs. 19, 27) 12
– Dorsal and ventral spine pairs subequal in size (Fig. 11); Colombia, Map 2 ..... *guerini*
12(11) Epigynum with projecting rounded lobe (Fig. 20); Ecuador, Map 2 ..... *pilaton*
– Epigynum with pointed lobe (Fig. 28); northern Colombia, Map 2 ..... *kochalkai*

Micrathena guerini (Keyserling) Figures 10–17; Map 2

Acrosoma guerinii Keyserling, 1863: 79, pl. 2, fig. 12, ♀. Female syntypes from Santa Fé de Bogota [Bogotá], Colombia (BMNH), examined. 1892: 22, pl. 1, fig. 18, ♀.

Micrathena guerini:—Reimoser, 1917: 124, pl. 7, fig. 21, ♀. Roewer, 1942: 959. Bonnet, 1957: 2870. Chickering, 1960c: 79, figs. 50–51, ♀.

Micrathena brunnea Mello-Leitão, 1941: 265, fig. 2, ♀. Female holotype from Bogotá, Colombia (MNRJ), lost. NEW SYNONYMY.

Synonymy. The description of *M. brunnea* fits that of *M. guerini*. The type localities of both are the same.

Description. Female. Carapace orange, thorax dark brown. Sternum orange-brown. Legs brown. Dorsum of abdomen whitish, spines orange-white; sides black with white patches; venter black. Carapace without dimples or rim; thorax high, almost coming to a point anterior of abdomen overhang. Abdomen with two pairs of posterior spines, dorsal ones longest (Fig. 11). Total length, 7.5 mm. Carapace, 2.9 mm long, 1.8 mm wide. First femur, 2.9 mm; patella and tibia, 2.9 mm; metatarsus, 1.7 mm; tarsus, 0.9 mm. Second patella and tibia, 2.7 mm; third, 1.6 mm. Fourth femur, 3.3 mm; patella and tibia, 2.9 mm; metatarsus, 2.0 mm; tarsus, 1.0 mm.

Male. Carapace orange, sides black. Sternum, coxae orange. Legs dusky orange, first darkest. Dorsum of abdomen with paired white marks, brownish gray and black; venter black. Carapace with a dimple on each side of thoracic depression, and a pair of indistinct dimples more anteriorly. First coxa with hook, second femur with groove. First and second tibia with macrosetae. Abdomen rectangular, with three pairs of small humps on posterior (Fig. 15). Total length, 5.6 mm. Carapace, 2.2 mm long, 1.4 mm wide. First femur, 1.9 mm; patella and tibia, 2.0

mm; metatarsus, 1.2 mm; tarsus, 0.7 mm. Second patella and tibia, 1.7 mm; third, 1.1 mm. Fourth femur, 2.0 mm, patella and tibia, 1.7 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm.

Variation. Females vary in total length from 6.7 to 8.4 mm, males from 5.3 to 5.6 mm. The dorsal abdominal spines are sometimes longer than the ventral. Some females have two pairs of very small humps on the sides of the abdomen. The type specimen has the anterior lobe of the epigynum constricted near its base.

Note. Males have been collected at the same locality as females near Saladito, Valle, Colombia.

Diagnosis. Females can be distinguished from others with anterior lobes on the epigynum by having only four spines of subequal length on the abdomen (Fig. 11); others have six. *Micrathena pilaton* has the dorsal spines longer. Males can be separated from others with a coxal hook by having a hump at the base of the cymbium above the paracymbium (Fig. 17), by the shape of the median apophysis, and by the shape of the conductor, which is folded over at its end (Fig. 16).

Natural History. The species is found in cloud forest.

Distribution. Colombia (Map 2).

Records. COLOMBIA: *Dept. Cundinamarca.* Pacho, 1910, ♀ (NMW). *Valle.* near Atuncela, 1,800 m, 23 Nov. 1969, ♀ (W. Eberhard, MCZ); El Silencia, nr. Cali, 2,000 m, July 1974, ♀ (W. Eberhard, MCZ); Queremal, 2,000 m, June 1977, ♀ (W. Eberhard, MCZ); above Saladito, 1,800 m, 20 March 1970, ♀ (W. Eberhard, MCZ), 3 Jan. 1977, ♀ (H. W. Levi, MCZ), April 1977, ♀, ♂; April 1979, ♀ (W. Eberhard, MCZ).

Micrathena pilaton new species
Figures 18–25; Map 2

Holotype. Female and male paratype from Río Pilatón, Pichincha Prov., Ecuador, Sept. 1944 (G. W. Prescott, MCZ).

Description. Female. Carapace blackish brown, head darkest, black sternum. Coxae brown, distal leg articles dark brown. Abdomen black, without marks. Carapace with very high thorax and thoracic mark. Abdomen with four spines, hardly sclerotized (Fig. 19). Total length, 6.5 mm. Carapace, 2.6 mm long, 1.9 mm wide. First femur, 2.9 mm; patella and tibia, 2.9 mm; metatarsus, 1.9 mm; tarsus, 1.0 mm. Second patella and tibia, 2.7 mm; third, 1.7 mm. Fourth femur, 3.2 mm; patella and tibia, 2.9 mm; metatarsus, 1.9 mm; tarsus, 0.9 mm.

Male. Carapace orange, sides of thorax brown. Legs orange-brown. Dorsum of abdomen dark in center, white on sides, venter black. Carapace dull, with microscopic pattern, a distinct thoracic depression and very shallow dimples. Second tibia with macrosetae. Sides of abdomen slightly convex; three pairs of tiny humps posteriorly (Fig. 23). Total length, 5.3 mm. Carapace, 2.2 mm long, 1.4 mm wide. First femur, 1.9 mm. Second patella and tibia, 1.0 mm; third, 0.9 mm. Fourth femur, 2.1 mm; patella and tibia, 1.8 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm.

Diagnosis. Micrathena pilaton can be separated from *M. guerini* by the dorsal spine pair on the abdomen, which is much

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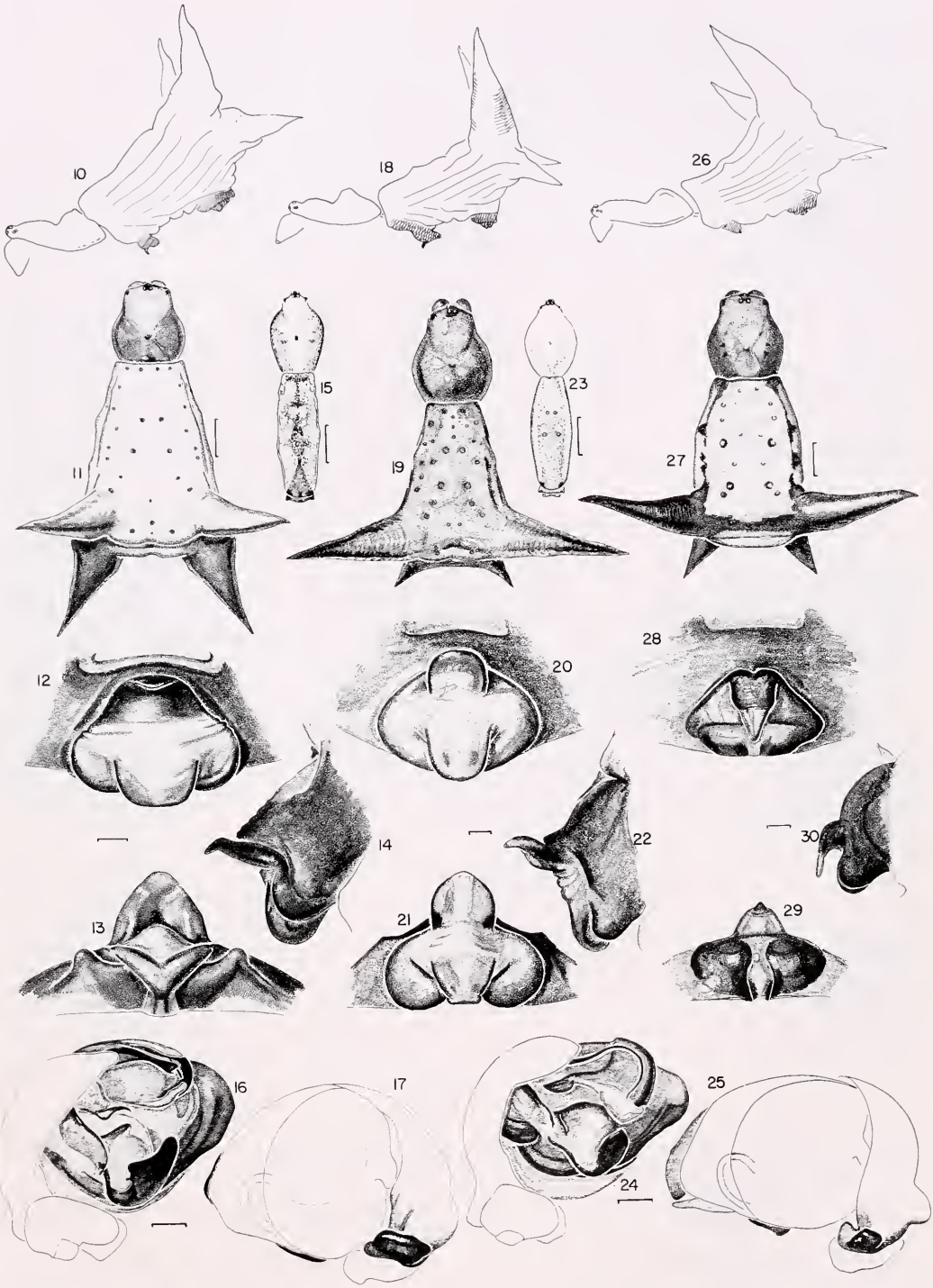
Figures 10–17. *Micrathena guerini* (Keyserling). 10–14. Female. 10. Lateral. 11. Dorsal. 12. Epigynum, ventral. 13. Epigynum, posterior. 14. Epigynum, lateral. 15–17. Male. 15. Dorsal. 16. Left palpus, mesal. 17. Palpus, lateral.

Figures 18–25. *Micrathena pilaton* n. sp. 18–22. Female. 18. Lateral. 19. Dorsal. 20. Epigynum, ventral. 21. Epigynum, posterior, 22. Epigynum, lateral. 23–25. Male. 23. Dorsal. 24. Palpus, mesal. 25. Palpus, lateral.

Figures 26–30. *Micrathena kochalkai* n. sp., female. 26. Lateral. 27. Dorsal. 28. Epigynum, ventral. 29. Epigynum, posterior. 30. Epigynum, lateral.

Scale lines. 0.1 mm, except Figures 10, 11, 15, 18, 19, 23, 26, 27, 1.0 mm.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longer than the ventral one (Fig. 19). The epigynum has slightly different proportions (Fig. 20) and appears different in posterior view (Fig. 21). Much more distinct is the structure of the male palpus, which convinces me that this is a separate species from *M. guerini*. The median apophysis is more gently lobed; a terminal apophysis is missing (perhaps it has been torn off) (Fig. 24). The hump on the cymbium is more distinct than that of *M. guerini* (Fig. 25).

Micrathena kochalkai new species
Figures 26–30; Map 2

Holotype. Female from Serra Nueva Granada, Sierra Nevada de Santa Marta, 1,930 m, Dept. Magdalena, Colombia (J. Kochalka, MCZ). The species is named after the collector.

Description. Female. Carapace orange, black on sides. Sternum orange, coxae lighter orange. Distal leg articles orange with gray pigment. Dorsum of abdomen light orange with black marks; spines black; venter black; area between booklungs light; area between epigynum and spinnerets orange. Carapace with three pairs of dimples, first pair least distinct; thoracic depression and high thorax. Posterior median eyes slightly larger than others, which are subequal. Abdomen with four spines (Figs. 26, 27). Total length, 7.4 mm. Carapace, 2.7 mm long, 2.2 mm wide. First femur, 3.0 mm; patella and tibia, 3.5 mm; metatarsus, 2.2 mm; tarsus, 0.9 mm. Second patella and tibia, 2.9 mm; third, 1.8 mm. Fourth femur, 3.5 mm; patella and tibia, 3.2 mm; metatarsus, 2.3 mm; tarsus, 0.9 mm.

Diagnosis. This species differs from *M. guerini* by the narrow, scapelike fold of the epigynum (Figs. 28, 30).

Micrathena atuncela new species
Figures 31–39; Map 2

Holotype. Female holotype and six female, one male paratypes from cloud forest, 1,800 m el., above Atuncela, Dept. Valle, Colombia, 23 Nov. 1969 (W. Eberhard, MCZ) (female paratypes, AMNH, BMNH). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace light brown, sides darker brown. Chelicerae dark brown. Sternum blackish brown. Legs dark brown, distal articles and fourth leg slightly darker. Dorsum of abdomen white with indistinct black pattern; spines brownish black; sides black with two dorsoventral rows of white spots; venter black with a median white patch behind spinnerets. Carapace with high thorax, a thoracic mark and narrow rim; lacking dimples (Fig. 31). Abdomen with three pairs of large spines and sides almost parallel (Fig. 32). Total length, 7.0 mm. Carapace, 2.3 mm long, 1.8 mm wide. First femur, 2.3 mm; patella and tibia, 2.4 mm; metatarsus, 1.7 mm; tarsus, 0.9 mm. Second patella and tibia, 2.2 mm; third, 1.4 mm. Fourth femur, 2.8 mm; patella and tibia, 2.4 mm; metatarsus, 1.8 mm; tarsus, 0.9 mm.

Male from type locality (having been dry and moldy at one time). Carapace, sternum, legs orange-gray. Dorsum of abdomen with black and white marks; venter black. Carapace without dimples; median thoracic depression distinct (Fig. 37). First coxa with small hook, second femur with proximal groove. First femur and tibia with macrosetae. Abdomen longer

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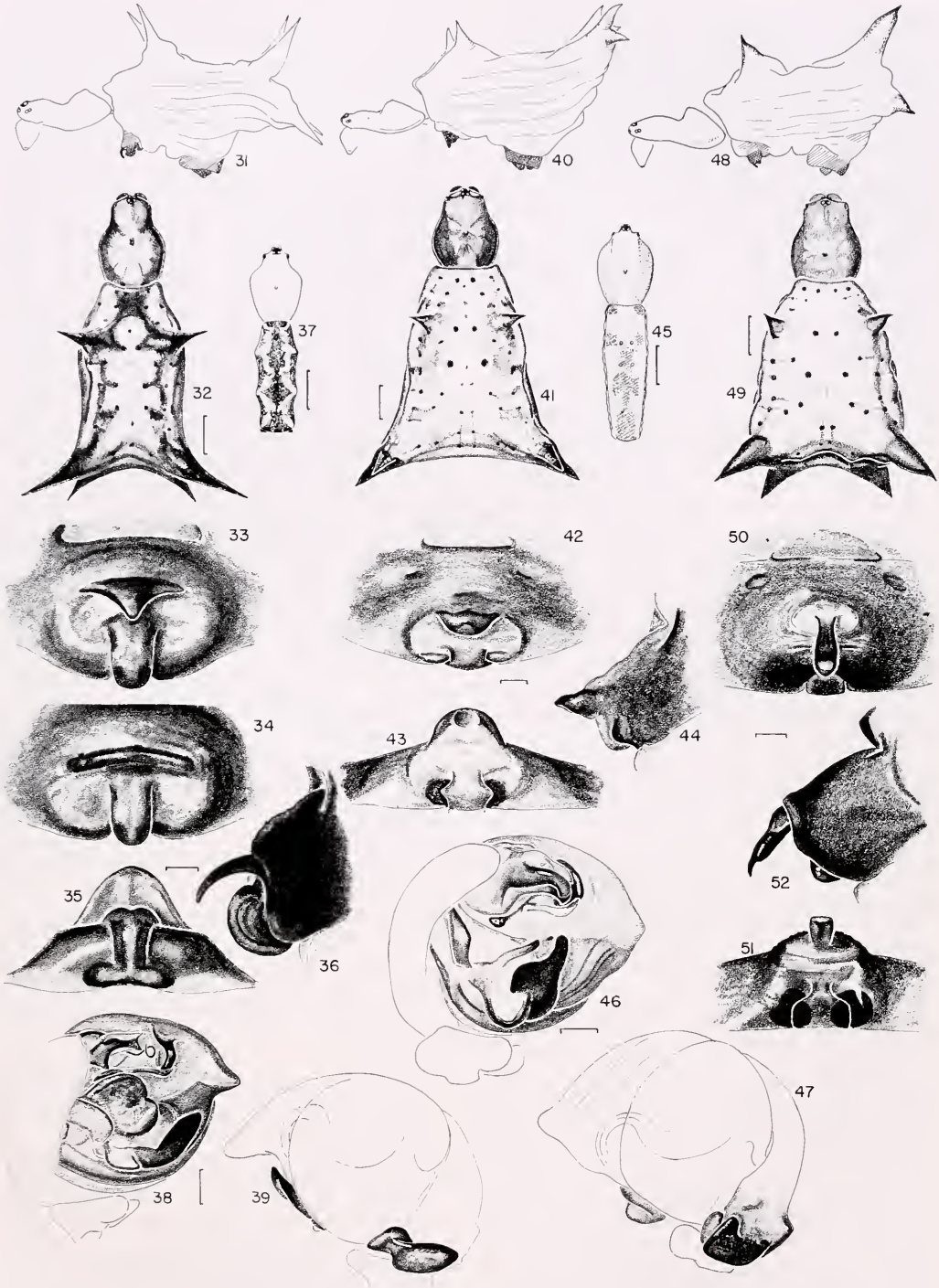
Figures 31–39. *Micrathena atuncela* n. sp. 31–36. Female. 31. Lateral. 32. Dorsal. 33, 34. Epigynum, ventral. 34. Lobe torn off. 35. Epigynum, posterior. 36. Epigynum, lateral. 37–39. Male. 37. Dorsal. 38. Left palpus, mesal. 39. Palpus, lateral.

Figures 40–47. *Micrathena bifida* (Taczanowski). 40–44. Female. 40. Lateral. 41. Dorsal. 42. Epigynum, ventral. 43. Epigynum, posterior. 44. Epigynum, lateral. 45–47. Male. 45. Dorsal. 46. Palpus, mesal. 47. Palpus, lateral.

Figures 48–52. *Micrathena rubicundula* (Keyserling), female. 48. Lateral. 49. Dorsal. 50. Epigynum, ventral. 51. Epigynum, posterior. 52. Epigynum, lateral.

Scale lines. 0.1 mm, except Figures 31, 32, 37, 40, 41, 45, 48, 49, 1.0 mm.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than wide, sides almost parallel, slightly scalloped, posteriorly with three pairs of humps (Fig. 37). Total length, 4.2 mm. Carapace, 1.9 mm long. Second patella and tibia, 1.3 mm; third, 0.9 mm. Fourth femur, 1.9 mm; patella and tibia, 1.6 mm; metatarsus, 1.3 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 6.8 to 7.3 mm.

Note. The anterior lobe of the epigynum may be torn off (Fig. 34), probably when mating.

Diagnosis. The female has one more pair of spines on the abdomen (Fig. 32) than does *M. guerini.* In posterior view, it differs from *M. guerini* by having the dorsal part of the epigynum wider (Fig. 35). Females differ by having a wide anterior lobe on the epigynum (Fig. 33); *rubicundula* has a scape, *M. bifida* a rounded lobe. Unlike *M. guerini,* the male's embolus has a coil near its tip (Fig. 38).

Natural History. All specimens were collected from cloud forest.

Paratypes. COLOMBIA: *Dept. Valle.* 21 km W of Cali, 20 March 1955, ♀ (E. I. Schlinger and E. S. Ross, CAS).

Micrathena bifida (Taczanowski)
Figures 40–47; Map 2

Acrosoma bifida Taczanowski, 1879: 112, pl. 1, fig. 29. Female lectotype here designated and two female paralectotypes from Amable María [Junín, Prov. Tarma], Peru (PAN), examined.

Micrathena bifida:—Reimoser, 1917: 112. Roewer, 1942: 954. Bonnet, 1957: 2862.

Description. Female lectotype. Carapace, sternum, legs orange-brown. Carapace darker on sides. Dorsum of abdomen white with indistinct black marks and darker spines; venter black with paired white patches. Carapace with narrow rim, circular thoracic depression, and three dimples on each side; thorax high (Fig. 40). Abdomen trapezoidal with a pair of spines one third from anterior end and a double spine on each posterolateral corner (Fig. 41). Total length, 8.5 mm. Carapace, 2.7 mm long, 2.0 mm wide. First femur, 2.5 mm; patella and tibia, 2.7 mm; metatarsus, 1.7 mm; tarsus, 0.8 mm. Second patella and tibia, 2.3 mm; third, 1.5 mm. Fourth femur, 2.8 mm; patella and tibia, 2.4 mm; metatarsus, 1.8 mm; tarsus, 0.8 mm.

Male. Carapace orange, black on sides. Sternum, coxae orange. Legs blackish orange. Dorsum of abdomen orange with some black and some tiny white pigment spots; venter orange, black on sides and some black behind spinnerets. Carapace with thoracic depression and three pairs of dimples, posterior ones indistinct. First coxa with hook; groove on proximal end of second femur. Sides of abdomen almost parallel, undulating (Fig. 45). Total length, 5.8 mm. Carapace, 2.4 mm long, 1.5 mm wide. First femur, 1.9 mm; patella and tibia, 1.9 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm. Second patella and tibia, 1.6 mm; third, 0.9 mm. Fourth femur, 1.9 mm; patella and tibia, 1.6 mm; metatarsus, 1.2 mm; tarsus, 0.5 mm.

Note. Males and females have been matched by a collection of four females, three males and two juveniles from Utcuyacu, Peru.

Diagnosis. Micrathena bifida females differ from *M. atuncela* by the short, rounded lobe of the epigynum (Fig. 42). Males differ by the distinctive shape of the median apophysis and terminal apophysis (Fig. 46).

Distribution. Andes of Peru (Map 2).

Records. PERU: *Dept. Junín.* Utcuyacu, 1,600–2,200 m, March 1948, 4♀, 3♂ (F. Woytkowski, AMNH). *Ucayali.* Boquerón, Aug. 1946, ♀ (F. Woytkowski, AMNH).

Micrathena rubicundula (Keyserling)
Figures 48–52; Map 2

Acrosoma rubicundulum Keyserling, 1863: 74, pl. 2, fig. 7. Female type from Santa Fé de Bogota, Neu Granada [Bogotá, Colombia] (BMNH), examined; 1892: 21, pl. 1, fig. 17, ♀.

Micrathena rubicundula:—Reimoser, 1917: 130. Roewer, 1942: 962. Bonnet, 1957: 2875. Chickering, 1960c: 87, figs. 80–82, ♀.

Micrathena lordotica Mello-Leitão, 1941: 267, fig. 4,

♀. Female holotype from Bogotá, Colombia (MNRJ), lost. NEW SYNONYMY.

Synonymy. Mello-Leitão's figures of *M. lordotica* and the description best match *M. rubicundulum*. Both come from the same locality.

Description. Female. Carapace light orange, sides blackish; posterior darker orange. Sternum blackish orange. Legs dusky on orange. Dorsum of abdomen white with spines dark orange, sides black, and venter black with two paraxial white lines. Carapace with thoracic mark and very high thorax; without dimples (Fig. 48). Abdomen with three pairs of large spines (Fig. 49). Total length, 7.0 mm. Carapace, 2.6 mm long, 1.8 mm wide. First femur, 2.3 mm; patella and tibia, 2.6 mm; metatarsus, 1.6 mm; tarsus, 0.8 mm. Second patella and tibia, 2.2 mm; third, 1.4 mm. Fourth femur, 2.6 mm; patella and tibia, 2.2 mm; metatarsus, 1.6 mm; tarsus, 0.8 mm.

Variation. Females vary in total length from 7.0 to 7.3 mm.

Note. The male is not known.

Diagnosis. Micrathena rubicundula differs from the other species in this group having six spines and a scapelike structure in the epigynum (*atuncela, gurupi, teresopolis* and *nigrichelis*) by the shape of the scape: narrow, elongate, constricted proximally and without annuli (Figs. 50, 52).

Distribution. Colombia, Ecuador (Map 2).

Records. ECUADOR: *Prov. Tungurahua.* Baños, 220–2,500 m, April 1939, ♀ (W. C. McIntyre, MCZ).

Micrathena nigrichelis Strand, new status
Figures 53–60; Map 2

Micrathena fissispina var. *nigrichelis* Strand, 1908: 4. Female holotype from Joinville, Santa Catarina, Brazil (SMF), examined. Strand, 1915: 12. Roewer, 1942: 957. Bonnet, 1957: 2867.

Micrathena henseli Reimoser, 1917: 121, pl. 7, fig. 19, ♀. Two female syntypes from Pôrto Alegre, Serra Geral, S. Cruz [Rio Grande do Sul], Brazil (NMW), examined. Roewer, 1942: 959. Bonnet, 1957: 2870. Camargo, 1950a: 450, figs. 1, 2, ♀, ♂. Chickering, 1960c: 79, figs. 52–57, ♀, ♂. NEW SYNONYMY.

Synonymy. Reimoser did not recognize Strand's description, which lacked illustrations, and thought his specimens belonged to a new species.

Description. Female. Carapace orange, thorax dusky on sides. Sternum with black pigment. Legs orange. Dorsum of abdomen orange-white, anterior half darker; sides with fine black pigment on orange; venter dusky on orange. Carapace with narrow rim, a median thoracic mark and three pairs of dimples, thorax low. First, second and fourth femora with short macrosetae. Abdomen with three pairs of spines and a minute spine below posteroventral spine (Figs. 53, 54). Abdomen soft and finely punctate. Total length, 8.0 mm. Carapace, 3.0 mm long, 2.3 mm wide. First femur, 3.5 mm; patella and tibia, 3.5 mm; metatarsus, 2.7 mm; tarsus, 0.9 mm. Second patella and tibia, 3.0 mm; third, 1.7 mm. Fourth femur, 4.3 mm; patella and tibia, 3.2 mm; metatarsus, 2.6 mm.

Male. Carapace orange-brown, dark on each side of thorax. Sternum blackish. First and second leg brown, third and fourth orange-gray. Dorsum of abdomen with some white marks on sides and black pigment patches; venter black. Carapace with three pairs of dimples, rims with minute teeth. First, second and fourth femora with short macrosetae. First coxa with hook, second femur with groove. Dorsum of abdomen covered with minute teeth and six small spines (Fig. 58). Total length, 5.3 mm. Carapace, 2.2 mm long, 1.4 mm wide. First femur, 2.2 mm; patella and tibia, 2.2 mm; metatarsus, 1.7 mm; tarsus, 0.6 mm. Second patella and tibia, 1.9 mm; third, 1.0 mm. Fourth femur, 2.4 mm; patella and tibia, 1.7 mm; metatarsus, 1.6 mm; tarsus, 0.6 mm.

Variation. Females vary in total length from 5.6 to 8.6 mm, males from 4.4 to 5.9 mm. Some males appear to mature after fewer instars than others. In females the tiny tooth below the third pairs of abdominal spines is often absent. Juveniles may

have three pairs of spines on the posterior end. Females from Teresópolis sympatric with *M. teresopolis* are small, with narrowed abdomen and have the two posterior spines on each side extended on a common stalk.

Note. Many collections have males and females together. The point of the median apophysis probably fits into the depression of the female's scape. The scape is not torn off when mating.

Diagnosis. The round scape of the epigynum (Figs. 55, 57) separates females of this species from all other *Micrathena*, including *M. teresopolis*. The bulging and projecting tegulum, the pointed median apophysis (Fig. 59), and six tiny spines on the abdomen (Fig. 58) separate the males from other species.

Natural History. Judging by the large number of individuals in collections, this species must be abundant wherever it occurs. It has been collected from forests, roadsides and shrubs.

Distribution. Southeastern Brazil to northern Argentina (Map 2).

Records. BRAZIL: *Est. Espírito Santo.* Santa Leopoldina (MZSP). *Rio de Janeiro.* Alto da Tijuca; Pico de Tijuca; Petrópolis; Niterói; Teresópolis; Nova Friburgo. *Minas Gerais.* Caxambú; Lavras. *São Paulo.* 33 km S of São Paulo; São Paulo; Alto da Serra; Pirassununga; Barueri; Salesópolis; São Bernardo; São Roque; Cantareira; Limeira; Botucatú; Mirassol; Guarulhos; Diadema; Jarinú; Monte Alegre; Rio Claro; Cosmópolis; Barueri; Eng. Marcilac. *Paraná.* Rolândia; Curitiba; Araucária; Rincão; Guarapuava. *Santa Catarina.* Blumenau. *Rio Grande do Sul.* Pôrto Alegre; Pelotas; São Leopoldo; Guaíba. URUGUAY: *Dept. Treinta y Tres.* Río Olimar, 25 km W Treinta y Tres. *Dept. Lavaleja.* Sección 11a. *Maldonado.* Sierra de los Animas. PARAGUAY: *Dept. Paraguarí.* Sapucaí. ARGENTINA: *Prov. Misiones.* Aguarai-Guazú; Punto Bemberg Pasarele. *Salta.* Cerro San Lorenzo; Santa María.

Micrathena teresopolis new species
Figures 61–65; Map 2

Holotype. Female with torn scape from Serra dos Orgãos, 1,000–8,000 m, Est. Rio de Janeiro, Brazil, 19 April 1965 (H. Levi, MZSP). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, coxae, legs orange. Chelicerae blackish. Labium, sternum and endites orange-brown. Dorsum of abdomen whitish with some gray marks on sides; sides, venter orange. Booklung covers and ring around spinnerets blackish. Carapace with a median thoracic depression; lighter rim and dimples indistinct. Abdomen with six large spines (Figs. 61, 62). Total length, 7.5 mm. Carapace, 2.6 mm long, 2.0 mm wide. First femur, 2.6 mm; patella and tibia, 2.6 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm. Second patella and tibia, 2.4 mm; third, 1.4 mm. Fourth femur, 2.9 mm; patella and tibia, 2.5 mm; metatarsus, 1.8 mm; tarsus, 0.8 mm.

Variation. Females vary in total length from 4.9 to 7.5 mm.

Note. Most paratypes have the tip of the scape torn off. The male is unknown.

Diagnosis. Unlike females of *M. nigrichelis*, the scape of the epigynum is narrow with parallel sides (Fig. 63). The dimples and rim of the carapace are less distinct than those of *M. nigrichelis*, and

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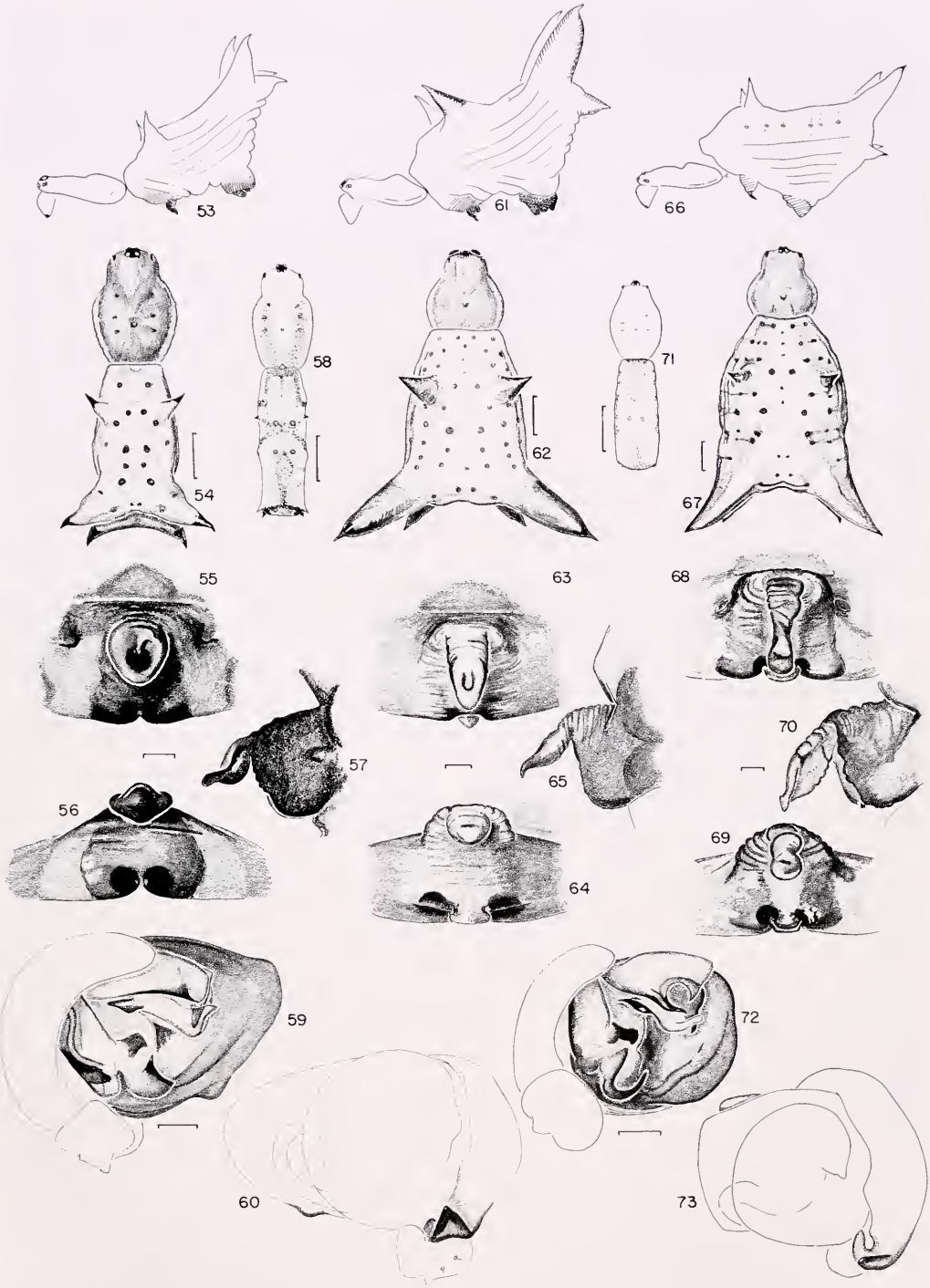
Figures 53–60. *Micrathena nigrichelis* Strand. 53–57. Female. 53. Lateral. 54. Dorsal. 55. Epigynum, ventral. 56. Epigynum, posterior. 57. Epigynum, lateral. 58–60. Male. 58. Dorsal. 59. Left palpus, mesal. 60. Palpus, lateral.

Figures 61–65. *Micrathena teresopolis* n. sp., female. 61. Lateral. 62. Dorsal. 63. Epigynum, ventral. 64. Epigynum, posterior. 65. Epigynum, lateral.

Figures 66–73. *Micrathena reali* n. sp. 66–70. Female. 66. Lateral. 67. Dorsal. 68. Epigynum, ventral. 69. Epigynum, posterior. 70. Epigynum, lateral. 71–73. Male. 71. Dorsal. 72. Palpus, mesal. 73. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 53, 54, 58, 61, 62, 66, 67, 71, 1.0 mm.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the upper posterior spines are longer than the ventral ones (Figs. 61, 62).

Natural History. Specimens have been collected in forest.

Distribution. Brazil, Est. Rio de Janeiro to São Paulo (Map 2).

Paratypes. BRAZIL: *Est. Rio de Janeiro.* Teresópolis, 7–9 Nov. 1945, 2♀, imm. (H. Sick, AMNH); Parque Nacional Itatiaia, 1,200 m, 4 April 1964, ♀ (C. E. and E. S. Ross, CAS); Serra dos Orgãos, 1,000–1,800 m, 19 April 1965, 8♀ (H. Levi, MCZ). *São Paulo.* São José do Barreiro, S. Bocaina, 1960 m, Nov. 1968, ♀ (M. Alvarenga, AMNH).

Micrathena reali new species
Figures 66–73; Map 2

Holotype. Female from Itaimbézinho, Est. Rio Grande do Sul, Brazil, 29 Dec. 1963 (Mauro C. Real, No. 01827, FZRS). The species is named after its collector.

Description. Female. Carapace, legs orange. Sternum dark orange, darker than coxae. Dorsum of abdomen white with gray marks on sides. Venter gray, white posteriorly. Carapace with distinct thoracic depression, indistinct rim, no dimples. Posterior median eyes slightly larger than others, which are subequal. Abdomen with six soft spines; posterior lower spines smaller than uppers (Figs. 66, 67). Total length, 8.1 mm. Carapace, 3.0 mm long, 2.3 mm wide. First femur, 2.8 mm; patella and tibia, 3.0 mm; metatarsus, 2.1 mm; tarsus, 0.9 mm. Second patella and tibia, 2.7 mm; third, 1.7 mm. Fourth femur, 3.2 mm; patella and tibia, 2.7 mm; metatarsus, 1.9 mm; tarsus, 0.7 mm.

Male. Carapace orange, sides of thorax slightly darker. Labium, endites, sternum black. Coxae and legs orange. Dorsum of abdomen with white pigment (Fig. 71), venter black. Carapace with three indistinct pairs of dimples and a thoracic depression. Coxal hook small; groove on proximal end of second femur. Abdomen in poor physical condition. Total length, 4.1 mm. Carapace, 1.7 mm long, 1.2 mm wide. First femur, 1.4 mm; patella and tibia, 1.4 mm; metatarsus, 1.0 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.8 mm. Fourth femur, 1.5 mm.

Variation. Females vary in total length from 6.7 to 8.1 mm. Of the seven specimens available, one had vague indication of dimples on the carapace and one had the scape torn off.

Note. The male comes from the same locality as females.

Diagnosis. This species differs from *M. nigrichelis* by lacking dimples on the carapace (Figs. 66, 67) and by having a narrow scape on the epigynum (Fig. 68). Unlike *M. teresopolis*, the scape has a neck and a dewlap (Figs. 68, 70). The male differs by having the median apophysis appear as a narrow hook in ventral view, and the terminal apophysis attached almost to the embolus tip (Fig. 72).

Distribution. Southeastern Brazil (Map 3).

Paratypes. BRAZIL: *Est. São Paulo.* Campos do Jordão, 15 Dec. 1944, March 1945, 3 Jan. 1948, 15 Dec. 1955, 22 Sept. 1961, 6♀ (nos. 4544, 4633, 8353, 8104, 6922, MZSP); March 1964, ♂ (F. Biasi, no. 3854, MZSP).

Micrathena shealsi Chickering
Figures 74–78; Map 2

Micrathena shealsi Chickering, 1960a: 8, figs. 13–17, ♀. Female holotype from Sunchal [? near Salta, Salta Prov.], Argentina (MCZ), examined.

Description. Female. Carapace orange with three dark brown longitudinal streaks, one through the middle and one on each side. Sternum, coxae light yellow; distal articles of legs orange. Dorsum of abdomen with white pigment in midline, blackish on sides; venter between epigynum and spinnerets yellow-white. Carapace with three pairs of dimples, a distinct thoracic depression and high thorax. The abdomen has six soft spines (Fig. 75). Total length, 8.2 mm. Carapace, 2.8 mm long, 2.0 mm wide. First femur, 2.9 mm; patella and tibia, 3.0 mm; metatarsus, 1.9 mm; tarsus, 0.9 mm. Second patella and tibia, 2.7 mm; third, 1.7 mm. Fourth fe-

mur, 3.3 mm; patella and tibia, 3.0 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm.

Note. It is uncertain whether the epigynum has had the scape torn off or lacks one altogether (Fig. 76). No other specimens similar to the type could be found in collections.

Diagnosis. This species was first thought to be *M. nigrichelis* with the scape of the epigynum torn off, but it differs by having a light sternum and a pigmentless median area on the venter of the abdomen.

Micrathena gurupi new species
Figures 79–83; Map 2

Holotype. Female from Canindé, Rio Gurupi, Est. Pará, Brazil, March–May 1964 (J. Carvalho, AMNH). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange-brown, rim white. Sternum dark brown, coxae lighter. Legs grayish brown. Dorsum of abdomen yellow-white with black marks; sides and venter black with white patches. Carapace with distinct thoracic depression. Femora tuberculate. Abdomen with six spines (Figs. 79, 80). Total length, 10.8 mm. Carapace, 3.6 mm long, 3.2 mm wide. First femur, 4.5 mm; patella and tibia, 4.3 mm; metatarsus, 3.3 mm; tarsus, 1.2 mm. Second patella and tibia, 3.6 mm; third, 2.1 mm. Fourth femur, 5.2 mm; patella and tibia, 4.4 mm; metatarsus, 3.7 mm; tarsus, 1.2 mm.

Variation. Females vary in total length from 9.2 to 11.0 mm.

Diagnosis. This species is larger than *Micrathena rubicundula.* It has a white rim around the carapace, and the scape of the epigynum is diamond-shaped (Figs. 81, 83).

Distribution. Suriname, northern Brazil (Map 2).

Paratypes. SURINAME: Republiek, June 1963, ♀ (P. H. van Doesburg, AMNH); Paramaribo, Aug. 1962, ♀ (P. H. van Doesburg, AMNH). BRAZIL: *Est. Pará.* Canindé, Oct. 1964, 2♀, 2 imm. (B. Malkin, AMNH), Feb.–March 1964, 2♀, 2 imm. (J. Carvalho, AMNH).

Micrathena bogota new species
Figures 84–88; Map 2

Holotype. Female and juvenile paratype are paralectotypes of *A. elongatus* Keyserling from Bogotá, Colombia (BMNH). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace with head yellow, sides of carapace orange. Chelicerae orange. Sternum, first coxae orange-brown with black pigment. Distal leg articles orange, first femur darkest, fourth lightest. Dorsum of abdomen with some paired black patches on white; sides with some indistinct dusky marks on posterior; venter with very distinct median black band having parallel sides, continuing into a black circle around spinnerets. Carapace with a distinct thoracic depression and a slight rim in dorsal view. Thorax relatively low. Posterior median eyes slightly larger than others, which are subequal. Abdomen longer than wide, with four pairs of spines (Figs. 84, 85). Total length, 7.5 mm. Carapace, 2.4 mm long, 1.9 mm wide. First femur, 2.2 mm; patella and tibia, 2.1 mm; metatarsus, 1.4 mm; tarsus, 0.8 mm. Second patella and tibia, 1.9 mm; third, 1.2 mm. Fourth femur, 2.5 mm; patella and tibia, 2.0 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm.

Note. The scape of the epigynum of the type is torn off (Fig. 86).

Diagnosis. This species differs from *M. pupa* and *M. agriliformis* by having only eight spines, and by the very different epigynum (Figs. 86–88), which allies *M. bogota* with *M. guerini* and *M. elongata. Micrathena bogota* differs from the similar *M. elongata* by having a seemingly wider scape (Fig. 86), and the base of the epigynum set off from the dorsum (Figs. 86, 88); in posterior view there is a distinct lobe on each side separated by the median piece (Fig. 87).

Micrathena elongata (Keyserling)
Figures 89–93; Map 2

Acrosoma elongatum Keyserling, 1863: 75, pl. 2, fig. 8, ♀. Female lectotype here designated from Santa

Fé de Bogota, New Granada [Bogotá, Colombia] (BMNH), examined. 1892: 22, pl. 1, fig. 19, ♀.
Micrathena elongata:—Reimoser, 1917: 97. Roewer, 1942: 957. Bonnet, 1957: 2866. Chickering, 1960c: 76, figs. 38–40, ♀.

Types. Paralectotypes belong to three different species: an immature *Wagneriana*, a female and two immature *M. pupa* (Simon), and a female and immature of *M. bogota* n. sp. Keyserling's description of a yellow sternum, high thorax and lateral grooves fits only the lectotype: eight spines excludes *M. pupa*. The other specimens may have been added to the vial at a later time.

Description. Female. Carapace orange, brown on sides of thorax. Sternum orange with white pigment spots. Legs orange-brown. Dorsum of abdomen white, glossy; posterior black. Sides blackish, venter black with indistinct white band on each side. Carapace with thoracic depression; thorax high, lateral rims indistinct in dorsal view. Sides of abdomen with rows of tiny sclerites but no grooves (Figs. 89, 90). Total length, 8.2 mm. Carapace, 2.2 mm long, 1.6 mm wide. First femur, 2.1 mm; patella and tibia, 2.2 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm. Second patella and tibia, 2.0 mm; third, 1.2 mm. Fourth femur, 2.5 mm; patella and tibia, 2.2 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm.

Diagnosis. This species, like *M. bogota*, differs from *M. agriliformis* and *M. pupa* by having eight small spines (Figs. 89, 90). It differs from *M. bogota* by having the scape of the epigynum narrower; the base is not set off (Figs. 91, 93); in posterior view there appear to be two openings, one on each side of the median piece (Fig. 92).

The *kirbyi* Group

Females of the *kirbyi* group are characterized by having an epigynum with a raised, T-shaped structure on the bulge: a transverse bar with a posteromedian lobe (Figs. 3–5). This may be modified into a transverse bar (Fig. 297) or into a triangular structure (Figs. 104, 112, 361, 378, 420). It is very similar in many species. Its profile is shaped like a bird's head (Figs. 5, 161, 180). The carapace has a distinct thoracic mark, a high thorax, and up to three pairs of dimples (Figs. 122, 123, 192, 193).

Males always have a hook on the first coxa, often on the distal posterior edge (Fig. 2), and a matching groove on the proximal end of the second femur, facing the hook (Fig. 1). Males associated with females of two species may lack hook and groove (*M. excavata, M. quadriserrata*). The hook is larger and more ventral on the coxae of *M. clypeata*. The palpus has a paramedian apophysis attached to the conductor, a rectangular median apophysis whose distal rim is sclerotized and bent over (Levi, 1978: fig. 40; Figs. 143, 155), and a terminal apophysis forming a flat, lightly sclerotized flap covering the embolus (Figs. 100, 108, 143, 155, 182).

The diagnostic features of species are the arrangement of the spines on the abdomen of the females and the genitalia of both sexes. Both the epigyna and palpi of many species are very similar, and only obscure details separate the species. In females the posterior view of the epigynum must be examined; in males, the conductor, embolus and terminal apophysis of the palpus. The paracymbium is quite similar

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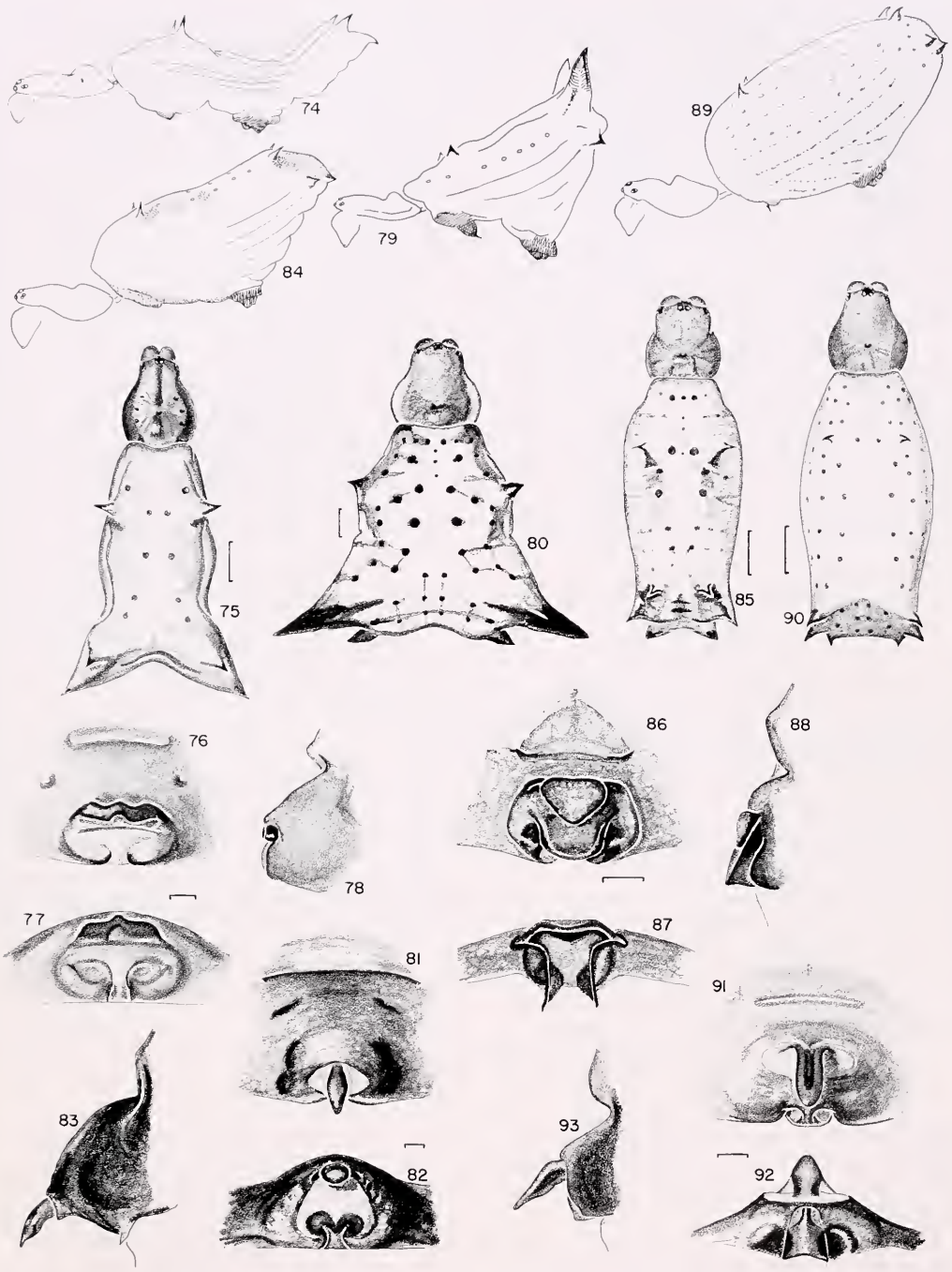
Figures 74–78. *Micrathena shealsi* Chickering, female. 74. Lateral. 75. Dorsal. 76. Epigynum, ventral, scape torn off. 77. Epigynum, posterior. 78. Epigynum, lateral.

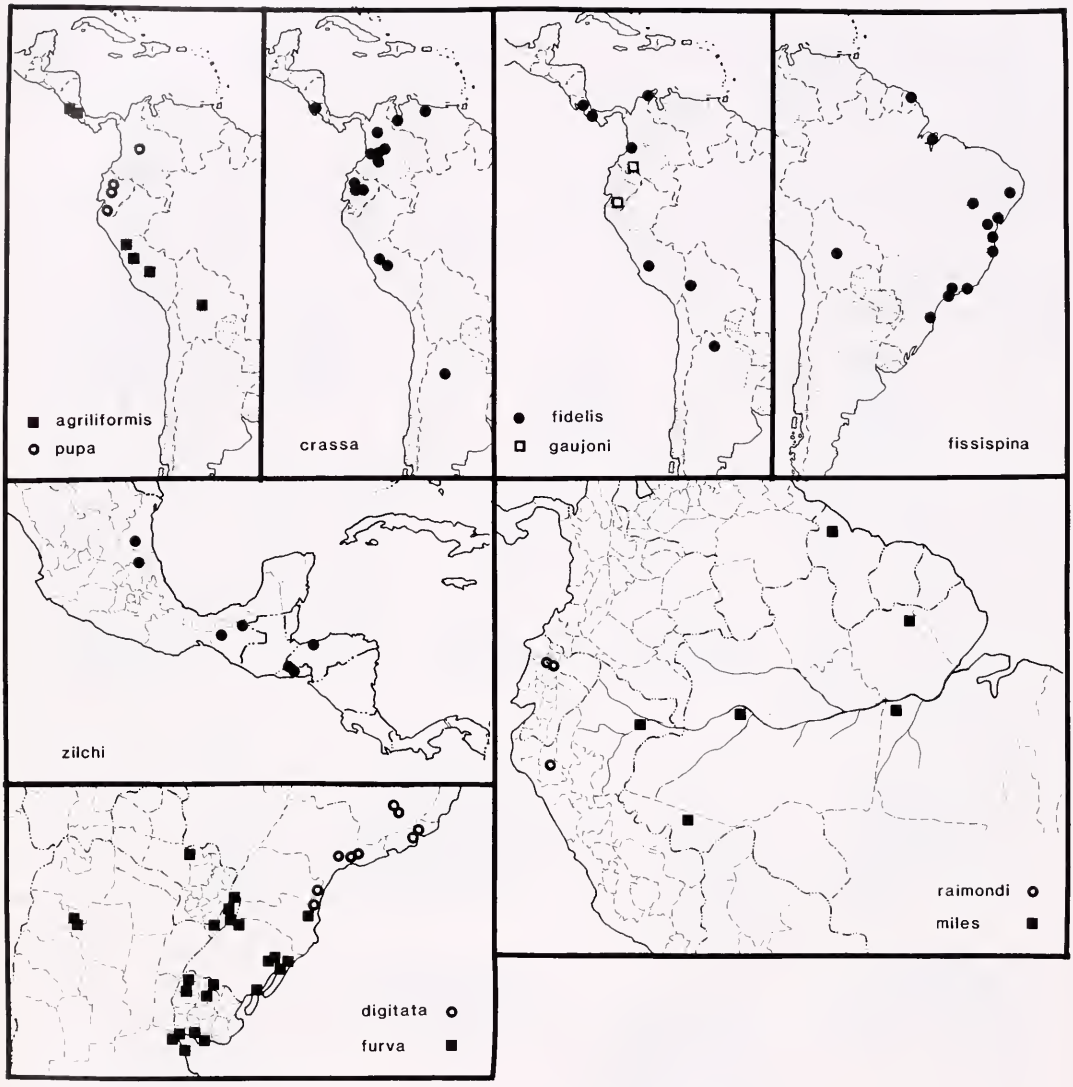
Figures 79–83. *Micrathena gurupi* n. sp., female. 79. Lateral. 80. Dorsal. 81. Epigynum, ventral. 82. Epigynum, posterior. 83. Epigynum, lateral.

Figures 84–88. *Micrathena bogota* n. sp., female. 84. Lateral. 85. Dorsal. 86. Epigynum, ventral, scape torn off. 87. Epigynum, posterior. 88. Epigynum, lateral.



Figures 89–93. *Micrathena elongata* (Keyserling), female. 89. Lateral. 90. Dorsal. 91. Epigynum, ventral. 92. Epigynum, posterior. 93. Epigynum, lateral.

Scale lines. 0.1 mm, except Figures 74, 75, 79, 80, 84, 85, 89, 90, 1.0 mm.



Map 3. Distribution of *Micrathena* species of the *kirbyi* group.

in most species (Figs. 101, 109). The median apophysis is also similar in many species, but its rim and lobe (Figs. 6, 9) may be diagnostic.

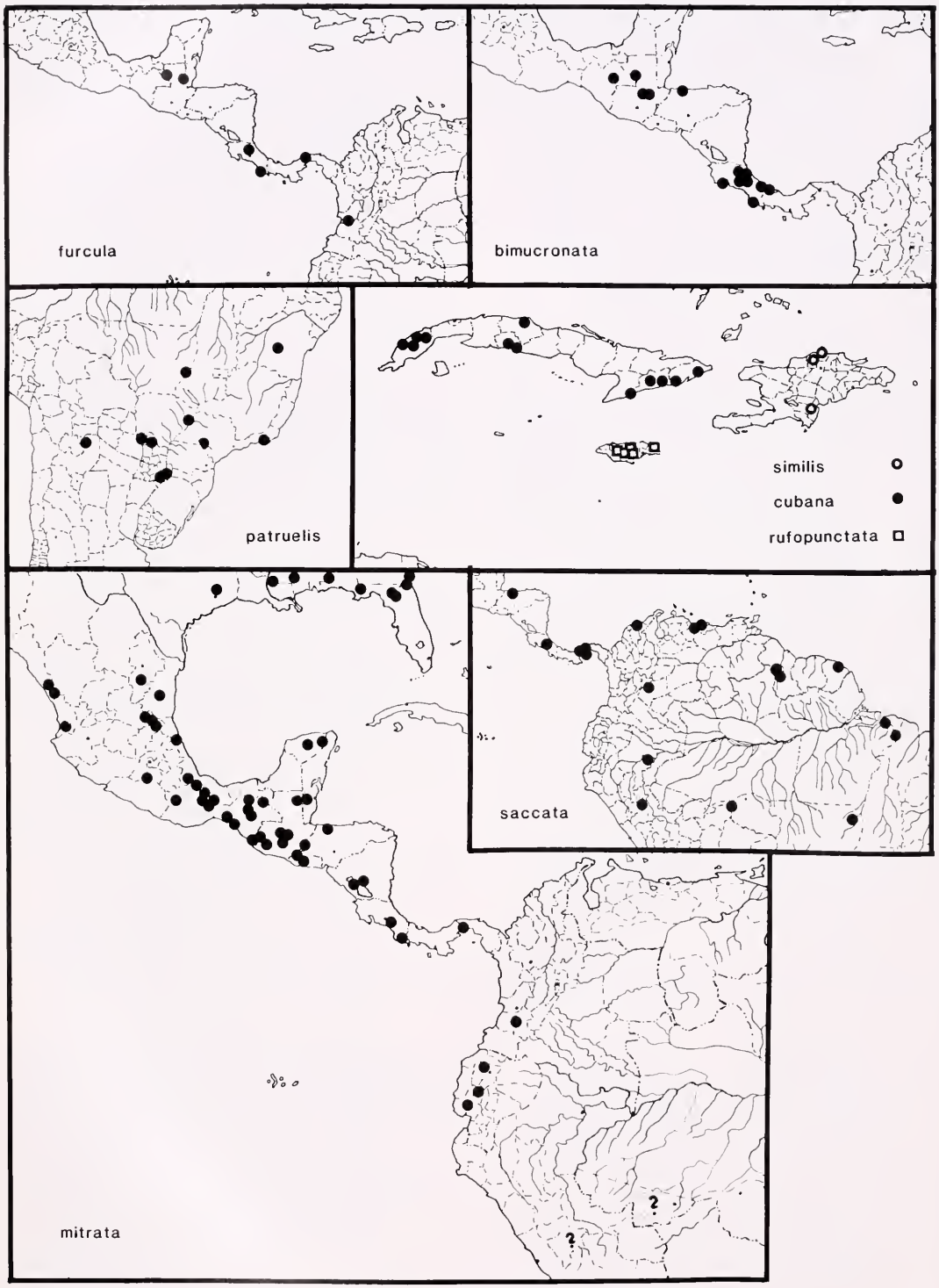
This is the largest species group, containing 45 species out of a total of 104.

KEY TO THE *KIRBYI* GROUP

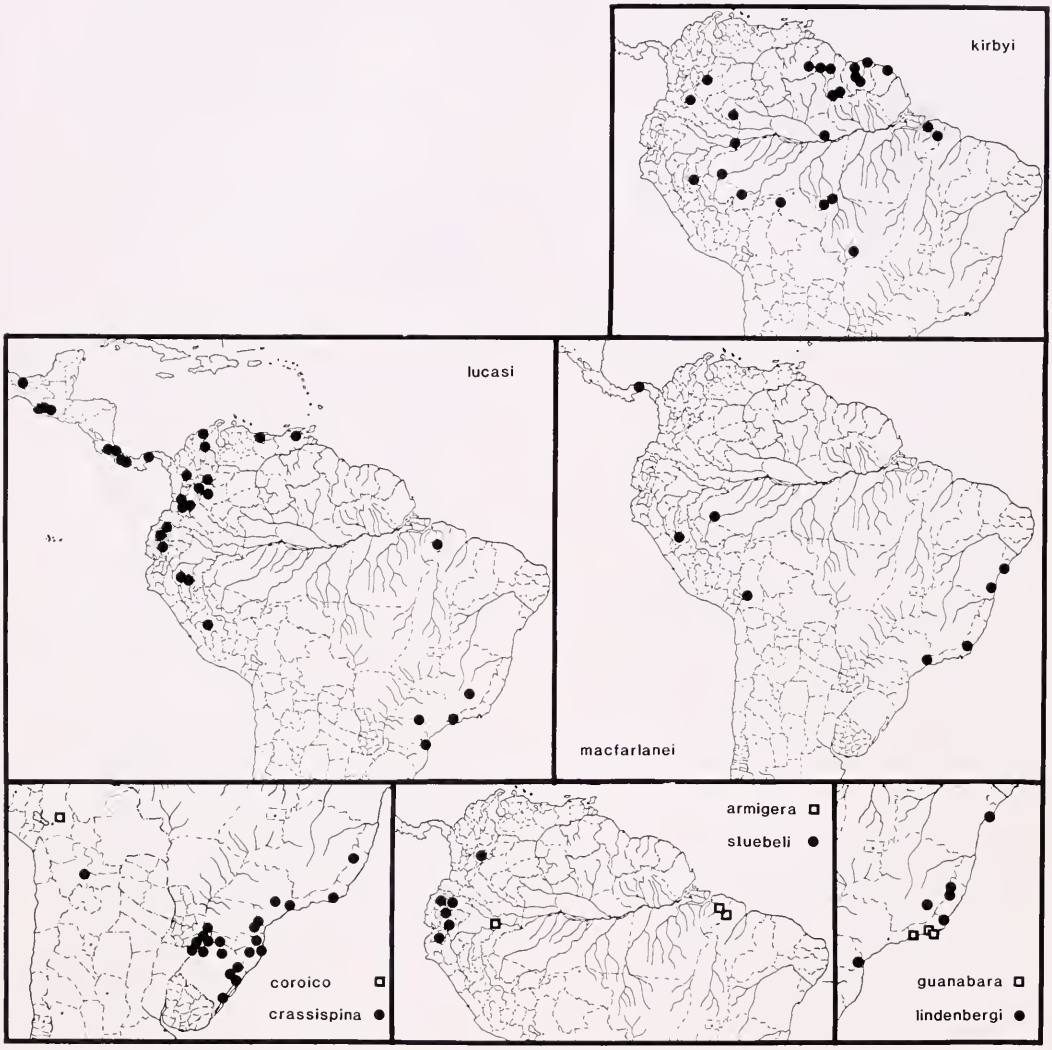
Females

1. No sharp spines on anterior of abdomen overhanging carapace (Figs. 103, 110, 123) (at most blunt tubercles; Figs. 116, 177, 184, 193) 2
– Spines on anterior of abdomen overhanging carapace (Figs. 231, 236, 243, 277) 20
2(1) Abdomen with 2 to 4 spines (Figs. 170, 177, 184, 193, 208) 3
– Abdomen with 6 or more spines or tubercles 10
3(2) Abdomen biforked or with 2 posterior spines (Figs. 170, 177, 184) 4
– Abdomen with 4 posterior spines (Figs. 193, 200, 208) 6

4(3) Abdomen biforked; carapace hairy (Fig. 170); Central America perhaps to Mato Grosso, Map 4 ..... *furcula*
– Abdomen with two spines; carapace glabrous (Figs. 177, 184) 5
5(4) Venter of abdomen with three pairs of red patches (Fig. 183); Jamaica, Map 4 ..... *rufopunctata*
– Venter of abdomen without light patches (Fig. 176); Central America, Map 4 ..... *bimucronata*
6(3) Upper spines longer than lower spines (Figs. 207, 208, 213, 214, 218, 219) 7
– Upper and lower spines subequal in length (Figs. 192, 193, 199, 200, 225, 226) 8
7(6) Dorsum of abdomen white with black pattern (Fig. 219); Cuba, Map 4 ..... *cubana*
– Dorsum of abdomen white to orange (Figs. 208, 214); Honduras to northern South America, Map 4 ..... *saccata*
8(6) Abdomen often with black pattern (Fig. 193); eastern North America to western South America, Map 4 ..... *mitrata*
– Dorsum of abdomen usually light, without pattern (Figs. 200, 226) 9
9(8) Epigynum with Y-shaped bar and lobe (Fig. 227); Hispaniola, Map 4 ..... *similis*
– Epigynum with straight transverse bar and a wide lobe (Fig. 201); southeastern Brazil to northern Argentina, Map 4 ..... *patruelis*
10(2) Abdomen with 6 spines 11
– Abdomen with 8 or more spines 12
11(10) Epigynum framed on each side (Figs. 158, 159); Ecuador, Peru, Map 3 ..... *raimondi*
– Epigynum not so framed, and with bar and lobe Y-shaped (Fig. 166); Amazon area, Map 3 ..... *miles*
12(10) Carapace with a deep transverse groove (Fig. 115); Central America, western South America to Argentina, Map 3 ..... *crassa*
– Carapace not so grooved (Figs. 102, 129, 144) 13
13(12) Abdomen with 8 long, thin spines (Figs. 110, 111); Mexico to Honduras, Map 3 ..... *zilchi*
– Abdomen with spines short (Figs. 103, 130, 150) 14
14(13) Abdomen length more than twice width, with 10 tiny spines (Figs. 95, 103) 15
– Abdomen at most only slightly longer than wide, with spines larger (Figs. 123, 130, 137, 145, 150) 16
15(14) Lobe of epigynum framed on each side by sclerotized cheeks (Fig. 104); Colombia, Ecuador, Map 3 ..... *pupa*
– Lobe of epigynum not so framed (Fig. 96); Costa Rica to Bolivia, Map 3 ..... *agriliformis*
16(14) Abdomen with one large spine on each side and 6 posteriorly (Figs. 145, 150) 17
– Abdomen with no spines on sides, or with one or two small ones on each side 18
17(16) Upper two posterior spines on a common stalk (Figs. 149, 150); eastern South America to Bolivia, Map 3 ..... *fissispina*
– Two lower posterior spines some distance from upper spines (Fig. 144); Colombia, Ecuador, Map 3 ..... *gaujoni*
18(16) Two spines posteriorly (Figs. 136, 137); Costa Rica to northern Argentina, Map 3 ..... *fidelis*
– Three spines posteriorly (Figs. 123, 129); southeastern South America 19
19(18) Upper posterior spines with a lobe (Figs. 122, 123) ..... *digitata*
– Upper posterior spine not lobed (Figs. 129, 130) ..... *furva*
20(1) Abdomen with 6 spines (Figs. 230, 231); Bolivia, Map 5 ..... *coroico*
– Abdomen with 8 to 12 spines 21
21(20) Abdomen with 8 spines (Figs. 235, 236, 242, 243, 406) (rarely with 10; *crassispina* with tiny 5th pair; *lucasi* with tiny 2nd pair) 22
– Abdomen with 10 or 12 spines; third pair sometimes minute 24
22(21) Epigynum with 2 light depressions on ventral face of semispherical bulge (Fig. 407); Chiapas, Map 6 ..... *lenca*
– Epigynum with usual transverse bar having a posterior median lobe (Figs. 237, 247) 23
23(22) Third and fourth spines originating from joint base on each side (Figs. 242–246); lobe of epigynum light colored and without frame on each side (Fig. 247), Mexico to southeastern Brazil ..... *lucasi*
– Third and fourth spines well separated and facing opposite directions (Fig. 235); lobe of epigynum dark, with a semicircular frame on each side (Fig. 237); southeastern Brazil to Bolivia, Map 5 ..... *crassispina*
24(21) Abdomen wider than long; fourth pair of spines with a posterior lobe (Figs. 276, 277); Colombia to Peru, Map 5 ..... *stuebeli*
– Abdomen longer than wide or as wide as long; none of spines with lobe 25
25(24) Abdomen with 10 spines (Figs. 253, 272, 419) 26
– Abdomen with 12 or more spines (Figs. 313, 327, 370, 395) 31
26(25) Dorsum of abdomen very flat; 10 thick spines around margin (Fig. 419); Panama, Colombia, Amazon area, Map 6 ..... *clypeata*
– Dorsum of abdomen otherwise (Figs. 253, 267, 272, 284) 27

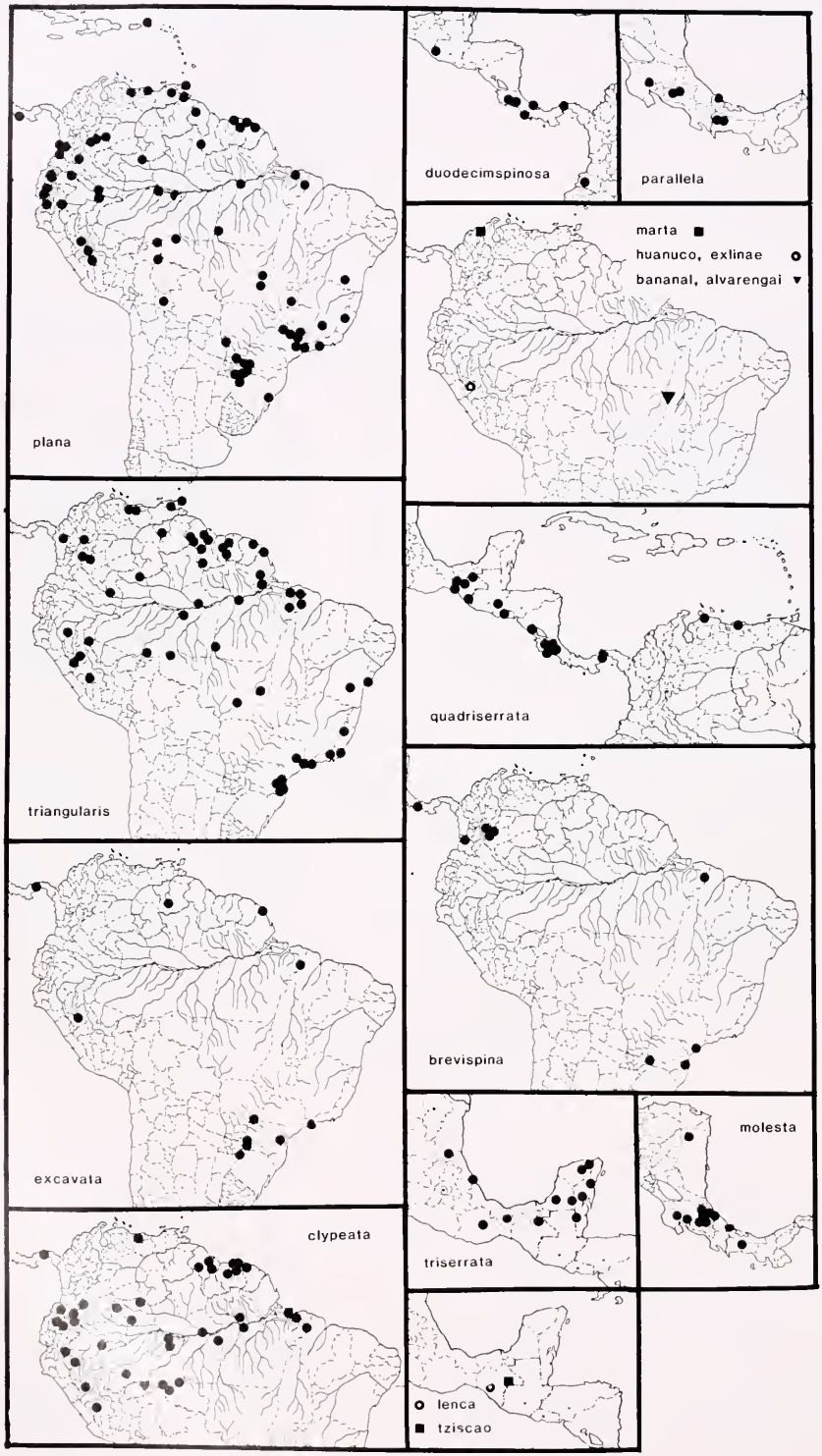


Map 4. Distribution of *Micrathena* species of the *kirbyi* group.



Map 5. Distribution of *Micrathena* species of the *kirbyi* group.

27(26) Three pairs of posterior spines; the two lower pairs some distance from upper (Figs. 271, 283); southeastern Brazil 28
– Two pairs of posterior spines (Figs. 252, 261, 266) 29
28(27) Abdomen narrow, slightly constricted between second and third pairs of spines (Fig. 272); transverse bar of epigynum not framed (Fig. 273); Map 5 ..... *lindenbergi*
– Abdomen wider, not constricted (Fig. 284); Map 5 ..... *guanabara*
29(27) Abdomen with black and white pattern as in Figures 266, 267; Guianas, Amazon, Map 5 ..... *kirbyi*
– Abdomen without such pattern 30
30(29) Transverse bar of epigynum short, anterior lip curved posteriorly on each side, framing lobe (Fig. 254); posterior view of epigynum with central flat, light area (Fig. 256); Panama, Peru to southeastern Brazil, Map 5 ..... *macfarlanei*
– Transverse bar straight and long; anterior lip not curved into a lateral frame


plana
duodecimspinosa
parallela
marta
huanuco, exlinae
bananal, alvarengai
quadriserrata
triangularis
brevispina
excavata
molesta
clypeata
triserrata
lenca
tziscao

(Fig. 263); posterior view of epigynum with a narrow, dark, swollen area (Fig. 264); Amazon area, Map 5 ..... *armigera*

31(25) Posterodorsal spines on wings separated by a notch (Figs. 370, 377, 387) 32

– Posterodorsal spines on corners of abdomen not separated by a distinct notch 34

32(31) Notch shallow (Fig. 370); transverse bar of epigynum without median lobe, almost narrower in middle (Fig. 371); Chiapas to Venezuela, Map 6 ..... *quadriserrata*

– Notch distinct (Figs. 377, 387); epigynum otherwise 33

33(32) Epigynum a triangular knob, often torn, framed on each side (Fig. 378, 379); Mexico, Guatemala, Map 6 ..... *triserrata*

– Epigynum with short transverse bar (Fig. 388); Panama to Argentina, Map 6 ..... *brevispina*

34(31) Venter of abdomen with a soft spine on each side of spinnerets (Fig. 347); 2nd, 3rd, 4th, 6th spine pairs dark, 5th pair light (Fig. 348); Panama to Argentina, Map 6 ..... *excavata*

– No such ventral spines; all spines the same color 35

35(34) Epigynum without transverse bar (Fig. 412), or bar forming a projecting lobe, usually torn off (Figs. 396–401); Chiapas to Panama 36

– Epigynum with transverse bar having usually a posterior median lobe 37

36(35) Epigynum a bulge with longitudinal grooves (Figs. 412–414); Chiapas, Map 6 ..... *tziscao*

– Epigynum with a median lobe (Figs. 396–398); usually torn off, leaving a transverse depression (Figs. 399–401); Nicaragua to Panama, Map 6 ..... *molesta*

37(35) Epigynum with subtriangular lobe, longer than wide (Fig. 361); abdomen with 14 spines (Figs. 359, 360); Goiás, Map 6 ..... *bananal*

– Epigynum otherwise 38

38(37) Anterior edge of transverse bar of epigynum swollen, convex (Figs. 315, 316, 356) 39

– Anterior edge of transverse bar concave or straight (Figs. 329, 330, 366) 40

39(38) Abdomen with a lobe between 2nd and 3rd spines (rarely, a small tooth before 2nd pair of spines) (Figs. 313, 314); Panama, West Indies to northern Argentina, Map 6 ..... *plana*

– Abdomen otherwise (Fig. 355), Map 6 ..... *marta*

40(38) Abdomen with 18 spines, 5 of equal size on each side (Figs. 364, 365); Goiás, Map 6 ..... *alvarengai*

– Abdomen with less than 18 spines or, if with 18, only four of equal size on each side 41

41(40) Posterodorsal spine trifid (Figs. 290, 291, 326) 42

– Posterodorsal spine bifid (Figs. 304, 337), or undivided (Fig. 342) 43

42(41) Two spines on each side between anterior and trifid spine (Figs. 292–295); Guatemala to Colombia, Map 6 ..... *duodecimspinosa*

– Three or more spines of equal size on each side between anterior and trifid spine (Figs. 327, 328); Colombia to southeastern Brazil, Map 6 ..... *triangularis*

43(41) Epigynum in posterior view with a light lobe on each side of median plate (Fig. 307); Costa Rica, Panama, Map 6 ..... *parallela*

– Posterior view of epigynum otherwise (Figs. 340, 345); Peru 44

44(43) Median plate of epigynum constricted ventrally in posterior view (Fig. 345); Map 6 ..... *exlinae*

– Median plate of epigynum with parallel sides in posterior view (Fig. 340); Map 6 ..... *huanuco*

Males

Note. The males for many species are unknown; for others the association with females is uncertain.

1. First coxa with hook on distal end (Fig. 2); second femur with proximal groove (Fig. 1) 3

– First coxa without hook; second femur without groove 2

2(1) Rim of median apophysis thorn-shaped (Fig. 353) ..... suspected male of *excavata*

– Rim with concave edge (Fig. 375); Chiapas to Venezuela, Map 6 ..... *quadriserrata*

3(1) Rim of median apophysis bearing narrow prong pointing to base of median apophysis (Fig. 424); abdomen barely longer than wide (Fig. 423); Panama to Amazon area, Map 6 ..... *clypeata*

– Rim of median apophysis otherwise 4

4(3) Lobe of median apophysis extended and

←

Map 6. Distribution of *Micrathena* species of the *kirbyi* group.

projecting (Figs. 416, 417); Chiapas, Map 6 ..... *tziscao*
– Lobe of median apophysis not extended 5
5(4) Abdomen with 6 spines (Fig. 58); southeastern Brazil to Argentina, Map 2 ..... *nigrichelis*
– Abdomen without spines 6
6(5) Rim of median apophysis wider than half its length (Figs. 121, 384, 403); species occurring in Mexico and Central America 7
– Rim of median apophysis not wider than half its length, or, if so, then species not occurring in Mexico or Central America 9
7(6) Rim of median apophysis with notch on inside margin (Fig. 121); Costa Rica to northern Argentina, Map 3 ..... suspected male of *crassa*
– Rim entire 8
8(7) Distal section of tegulum pointed (Fig. 403, upper right); upturned sclerotized hook at tip of embolus (Fig. 403); Nicaragua to Panama, Map 6 ..... *molesta*
– Distal section of tegulum rounded (Fig. 384); tip of embolus turned down (Fig. 384); Mexico to Guatemala, Map 6 ..... *triserrata*
9(7) Rim of median apophysis extended into a finger (Fig. 46); Peru, Map 2 ..... suspected male of *bifida*
– Rim otherwise 10
10(9) Embolus exposed (Figs. 16, 25, 38, 375) or covered by parallel, sclerotized terminal apophysis (Figs. 16, 375) 11
– Embolus covered in part by transparent, flat terminal apophysis (Figs. 59, 100, 205); only short pieces of embolus exposed 14
11(10) Embolus with a distal coil (Fig. 38); Colombia, Map 2 ..... *atuncela*
– Embolus tip not coiled 12
12(11) Embolus and surrounding area as in Figure 375; Chiapas to Venezuela, Map 6 ..... *quadriserrata*
– Embolus and surrounding area otherwise (Figs. 16, 25); South America 13
13(12) Embolus filiform, distally curved (Fig. 24); Ecuador, Map 2 ..... *pilaton*
– Embolus heavy and straight (Fig. 16); Colombia, Map 2 ..... *guerini*
14(10) Radix with "upper" lobe (Fig. 303, on left, close to cymbium edge); Guatemala to Colombia, Map 6 ..... *duodecimspinosa*
– Radix with margin straight 15
15(14) Embolus looping "above" terminal apophysis (Figs. 212, 325) 16
– Embolus with, at most, only tip exposed (Figs. 143, 163) 17
16(15) Wide terminal apophysis S-curved and gently narrowing to tip (Fig. 325); Central America, West Indies to Argentina, Map 6 ..... *plana*
– Narrow terminal apophysis, bent near base (Fig. 212); Honduras to Amazon area, Map 4 ..... *saccata*
17(15) Terminal apophysis with a round distal notch (Fig. 72); southeastern Brazil, Map 2 ..... *reali*
– Terminal apophysis without such distal notch 18
18(17) Terminal apophysis widening distally and truncate; median apophysis rim forming a spine (Fig. 282); Colombia, Ecuador, Map 5 ..... suspected male of *stuebeli*
– Terminal apophysis and median apophysis otherwise 19
19(18) Terminal apophysis with an "upper" lobe above cymbium (Fig. 241, upper left); southeastern Brazil to Bolivia, Argentina, Map 5 ..... *crassispina*
– Terminal apophysis without such a lobe 20
20(19) Tip of embolus extended beyond tip of terminal apophysis (Figs. 100, 108, 143, 224, 289) 21
– Tip of embolus not showing 25
21(20) Embolus tip biforked (Fig. 224); Cuba, Map 4 ..... *cubana*
– Embolus not forked 22
22(21) Embolus tip long and filiform (Fig. 108) ..... suspected male of *pupa*
– Embolus tip short (Figs. 100, 143, 289) 23
23(22) Embolus tip curved (Fig. 143) ..... suspected male of *fidelis*
– Embolus tip straight (Figs. 100, 289) 24
24(23) Embolus filiform (Fig. 289); southeastern Brazil, Map 5 ..... *guanabara*
– Embolus thick (Fig. 100) ..... suspected male of *agriliformis*
25(20) Conductor showing as a triangular sclerite "below" tip of terminal apophysis (Fig. 336); Venezuela, Colombia to southeastern Brazil, Map 6 ..... *triangularis*
– Conductor otherwise 26
26(25) Terminal apophysis relatively small, distal half narrow (Figs. 128, 135); southeastern Brazil 27
– Terminal apophysis otherwise 28
27(26) Conductor its width distant from cymbium (Fig. 128); Map 3 ..... *digitata*
– Conductor one and a half times its width distant from cymbium (Fig. 135); Map 3 ..... *furva*
28(26) Rim of median apophysis very large, a tiny notch on distal margin, and lobe almost absent (Fig. 121) ..... suspected male of *crassa*
– Median apophysis otherwise 29

29(28) Conductor visible as a drop-shaped structure; median apophysis with rim pointed (Fig. 155); eastern South America, Bolivia, Map 3 ..... *fissispina*
– Conductor and median apophysis otherwise 30

30(29) Bulb wider than long, with tegulum pointed "above" (Fig. 310, upper right); Costa Rica, Panama, Map 6 ..... *parallela*
– Bulb shorter, with tegulum rounded "above" 31

31(30) Terminal apophysis with "upper" border concave or with shallow notch 32
– Terminal apophysis otherwise 35

32(31) Terminal apophysis with three lobes (Fig. 182); Chiapas to Panama, Map 4 ..... *bimucronata*
– Terminal apophysis not so lobed 33

33(32) Upper margin of terminal apophysis straight, with shallow distal notch (Fig. 175); Guatemala to Colombia, Map 4 ..... *furcula*
– Upper margin of terminal apophysis curved (Figs. 198, 205, 206) 34

34(33) Truncate distal end of terminal apophysis turned "up" (Fig. 198); eastern U.S. to western South America, Map 4 ..... *mitrata*
– Distal end of terminal apophysis pointing "down" (Figs. 205, 206); southeastern Brazil to northern Argentina, Map 4 ..... *patruelis*

35(31) Terminal apophysis with distal point folded over (Fig. 163); rim of median apophysis with wide, shallow notch (Fig. 163); Ecuador, Peru, Map 3 ..... *raimondi*
– Terminal apophysis otherwise; median apophysis without such notch 36

36(35) Base of median apophysis sclerotized and sculptured (Figs. 259, 260, 289) 37
– Base of median apophysis not sclerotized (Figs. 251, 393) 38

37(36) Conductor holding tip of embolus in a shallow, curved dish (Fig. 289); southeastern Brazil, Map 5 ..... *guanabara*
– Conductor otherwise (Figs. 259, 260); Panama to southeastern Brazil, Map 5 ..... *macfarlanei*

38(36) Terminal apophysis with a sclerotized, pointed tip (Fig. 393); median apophysis square (Fig. 393); Panama to southeastern Brazil, Map 6 ..... *brevispina*
– Terminal apophysis with truncate, overhanging appendage (Fig. 251); median apophysis longer than wide (Fig. 251); Mexico to southeastern Brazil, Map 5 ..... *lucasi*

Micrathena agriliformis (Taczanowski)
Figures 94–101; Map 3

Acrosoma agriliformis Taczanowski, 1879: 119, pl. 11, fig. 33, ♀. Female lectotype here designated from Paltaypampa, male paralectotype from Pumamarca [both Dept. Junín, Prov. Tarma], Peru (PAN), examined.

Araneus agriliformis:—Simon, 1895: 858. Bonnet, 1955: 425.

Note. Reimoser (1917) considered Taczanowski's description unrecognizable. It is only listed in Reimoser's index. Roewer does not list this species; Bonnet places it in *Araneus*.

Description. Female. Carapace brown, sides of thorax darker. Sternum dark brown. Legs brown, coxae and femora lightest, distal articles darker. Dorsum of abdomen all white with black patches (Fig. 95); sides black, venter black without marks. Thoracic depression circular. Abdomen much longer than wide, soft, with five pairs of tiny spines (Figs. 94, 95). Total length, 7.5 mm. Carapace, 2.0 mm long, 1.5 mm wide. First femur, 1.9 mm; patella and tibia, 1.9 mm; metatarsus, 1.2 mm; tarsus, 0.7 mm. Second patella and tibia, 1.7 mm; third, 1.1 mm. Fourth femur, 2.1 mm; patella and tibia, 1.7 mm; metatarsus, 1.0 mm; tarsus, 0.7 mm.

Male paralectotype. Carapace, sternum dark brown. Legs brown, coxae and femora lighter, distal articles dark. Dorsum of abdomen dark with very little white pigment; sides, venter black. First coxa with hook. First and second femur and tibia with macrosetae, the second more strongly armed. Abdomen longer than wide (Fig. 99). Total length, 4.5 mm. Carapace, 1.8 mm long, 1.3 mm wide. First femur, 1.5 mm; patella and tibia, 1.4 mm; metatarsus, 0.8 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.7 mm. Fourth femur, 1.6 mm; patella and tibia, 1.3 mm; metatarsus, 0.8 mm; tarsus, 0.5 mm.

Note. The original collection had males and females matched. A male from Peru was with a penultimate instar female. The many males and few females collected

make me uncertain of this species. Are some males those of *M. fidelis*?

Diagnosis. Females differ from *M. pupa* by the shape of the epigynum, having the transverse bar V-shaped (Fig. 96). The male differs from *M. pupa* by having a shorter embolus (Fig. 100), and from both *M. pupa* and *M. fidelis* by having the embolus pass under the middle of the terminal apophysis (Fig. 100) in mesal view. The sclerotized rim of the median apophysis is relatively smaller (Fig. 100).

Distribution. Costa Rica to Bolivia, in mountains (Map 3).

Records. COSTA RICA: *Prov. Puntarenas.* Bosque Nuboso, Monteverde, cloud forest, 1,580 m el., 22 July 1978, ♂, imm. (C. L. Craig, P. Klass, MCZ). *San José.* Pico Blanco, above Escazú, 2,000 m, March 1983, ♂ (W. Eberhard, MCZ). PERU: *Huánuco Dept.* Carpish Mts., 51 km NE of Huánuco, 28 Dec. 1954, juv. ♀, ♂ (E. I. Schlinger, E. S. Ross, CAS). *Cuzco.* above Machu Pichu, 2,600–2,800 m, 1–5 July 1964, ♂ (B. Malkin, AMNH). BOLIVIA: *Dept. Cochabamba.* Sihuencas, 2,200 m el., Los Yungas, 25 Sept. 1953, 6♀ (W. Forster, ZSM).

Micrathena pupa Simon
Figures 102–109; Map 3

Micrathena pupa Simon, 1897b: 469. Twelve female, one male and juvenile syntypes from Loja, Ecuador (No. 10553, MNHN), examined and relabeled. Reimoser, 1917: 131. Roewer, 1942: 962. Bonnet, 1957: 2875.

Note. The left palpus of the male syntype is lost.

The illustrations were made from a female from Bogota, Colombia, a paralectotype of *Acrosoma elongata* Keyserling in the BMNH, and a male from Tungurahua, Ecuador. This male had the basal hematodocha slightly expanded, but in the illustration the bulb and cymbium were placed in their unexpanded position.

Description. Female syntype. Carapace brown, light in head region, slightly darker on sides of thorax. Sternum dark brown. Coxae, legs light. Dorsum of abdomen soft, shiny white with gray and black streaks; sides with a longitudinal band from anterior to posterior dorsal spine; venter black between spinnerets and epigynum, gray below pedicel. Thoracic depression circular; lacking dimples and rim. Abdomen with ten small spines: one anterior pair in middle on sides and three posterior pairs (Figs. 102, 103). Total length, 7.3 mm. Carapace, 2.5 mm long, 1.8 mm wide. First femur, 1.8 mm; patella and tibia, 1.9 mm; metatarsus, 1.1 mm; tarsus, 0.7 mm. Second patella and tibia, 1.8 mm; third, 1.1 mm. Fourth femur, 2.2 mm; patella and tibia, 1.7 mm; metatarsus, 1.2 mm; tarsus, 0.7 mm.

Male syntype. Coloration like female. Thoracic depression distinct. First coxa with small hook, second femur with groove. Abdomen with sides parallel anteriorly, narrowing posteriorly, with a slight notch at the posterior end (Fig. 107). Total length, 4.5 mm. Carapace, 1.9 mm long, 1.7 mm wide. First femur, 1.5 mm; patella and tibia, 1.5 mm; metatarsus, 0.8 mm; tarsus, 0.4 mm. Second patella and tibia, 1.3 mm; third, 0.7 mm. Fourth femur, 1.5 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm.

Variation. Females vary in total length

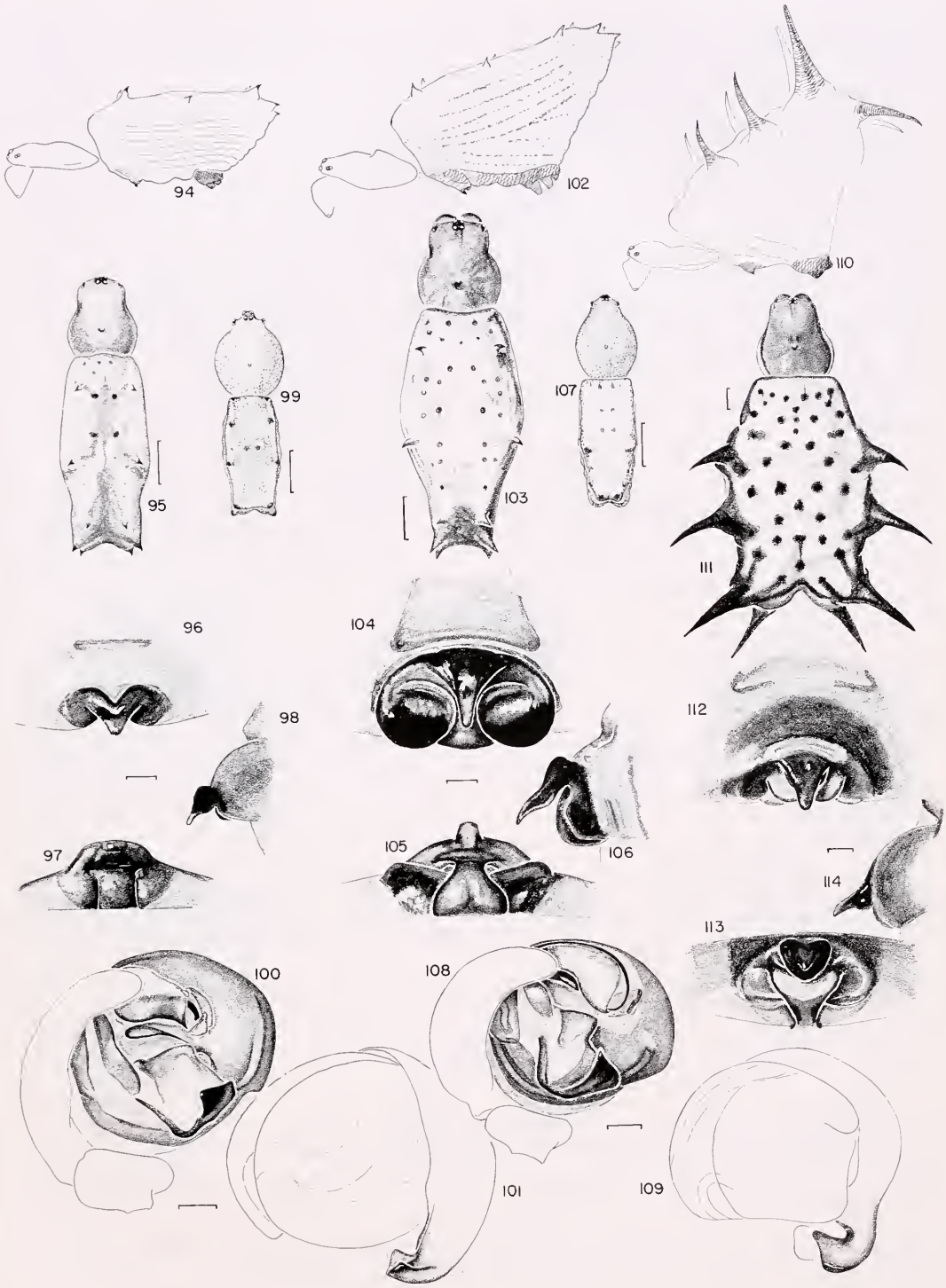
→

Figures 94–101. *Micrathena agriliformis* (Taczanowski). 94–97. Female. 94. Lateral. 95. Dorsal. 96. Epigynum, ventral. 97. Epigynum, posterior. 98. Epigynum, lateral. 99–101. Male 99. Dorsal. 100. Left palpus, mesal. 101. Palpus, lateral.

Figures 102–109. *Micrathena pupa* Simon. 102–106. Female. 102. Lateral. 103. Dorsal. 104. Epigynum, ventral. 105. Epigynum, posterior. 106. Epigynum, lateral. 107–109. Male. 107. Dorsal. 108. Palpus, mesal. 109. Palpus, lateral.

Figures 110–114. *Micrathena zilchi* Kraus, female. 110. Lateral. 111. Dorsal. 112. Epigynum, ventral. 113. Epigynum, posterior. 114. Epigynum, lateral.

Scale lines. 0.1 mm, except Figures 94, 95, 99, 102, 103, 107, 110, 111, 1.0 mm.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from 7.3 to 7.4 mm, males from 4.5 to 4.6 mm.The female from west of Quito has the lateral sclerotized areas of the epigynum straight rather than convex.

Note. Simon's original collection contained females with adult males. There is no reason to doubt the match.

Diagnosis. Micrathena pupa differs from the similar *M. agriliformis* by having the transverse bar of the epigynum straight, forming a triangle with the lobe (Fig. 104); *M. agriliformis* has it notched. Males have a thin threadlike embolus (Fig. 108), while *M. agriliformis* has a thick, only slightly curved embolus.

Distribution. Colombia to Ecuador, in mountains (Map 3).

Records. COLOMBIA: *Dept. Cundinamarca.* Bogotá, ♀ (Keyserling coll., BMNH). ECUADOR: *Tungurahua Prov.* Tungurahua, 2,600 m, 6 May 1939, 2♂ (W. Clarke-Macintyre, AMNH). *Pichincha.* 50 km W of Quito, 2,100 m, ♀ (L. Peña, MCZ).

Micrathena zilchi Kraus
Figures 110–114; Map 3

Micrathena zilchi Kraus, 1955: 29, pl. 4, figs. 76–78, ♀. Female holotype, 17 female paratypes from Volcán Las Naranjos, 1,600 m, El Salvador (SMF), examined.

Description. Female paratype. Carapace dark brown, head lightest; rim white. Sternum blackish brown, legs black. Dorsum of abdomen yellow-white with black marks and black spines; sides with longitudinal black bands towards spinnerets and additional ones crossing; venter with paired white patches on black. Carapace with median thoracic mark and narrow rim; no dimples. Abdomen with eight sharp sclerotized spines (Fig. 111). Total length, 12.6 mm. Carapace, 3.6 mm long, 3.6 mm wide. First femur, 5.1 mm; patella and tibia, 5.2 mm; metatarsus, 3.5 mm; tarsus, 1.3 mm. Second patella and tibia, 4.6 mm; third, 2.7 mm. Fourth femur, 5.4 mm; patella and tibia, 5.0 mm; metatarsus, 3.2 mm; tarsus, 1.2 mm.

Variation. Females vary in total length from 10.8 to 12.6 mm. While the triangular tip of the epigynum is alike in various specimens, the surrounding area is quite variable.

Note. The male is unknown. Immature females, probably pre-adult, have the same spines as the adult.

Diagnosis. Micrathena zilchi can be separated from others of this group by the dark triangular scape in the epigynum (Fig. 112) and by the eight sharp, long spines of the abdomen; the abdomen lacks spines on the anterior margin (Figs. 110, 111).

Distribution. Northeastern Mexico to El Salvador (Map 3).

Records. MEXICO: *Est. Tamaulipas.* 25 km N Gomez Farías, Jan. 1972, ♀ (W. Russell, AMNH); 13 km NW of Gomez Farías, 1,400 m, 6–7 Oct. 1965, 4♀ (B. Whitehead, AMNH). *San Luis Potosí.* El Salto, 11 km NW of El Naranjo, Sept., Nov. 1964, 3♀ (D. Whitehead, MCZ). *Chiapas.* El Vergel, 800 m, 8 Oct. 1939, ♀ (C. Bolivar and D. Pelaez, AMNH); Palenque ruins, July 1983, ♀ (W. Maddison, R. S. Anderson, MCZ). EL SALVADOR: *Dept. Santa Ana.* Candelaria, 31 Aug. 1953, juv. (B. Malkin, AMNH). HONDURAS: mountain trail [? near Tela], 360 m, 22 July 1929, imm. (A. M. Chickering, MCZ).

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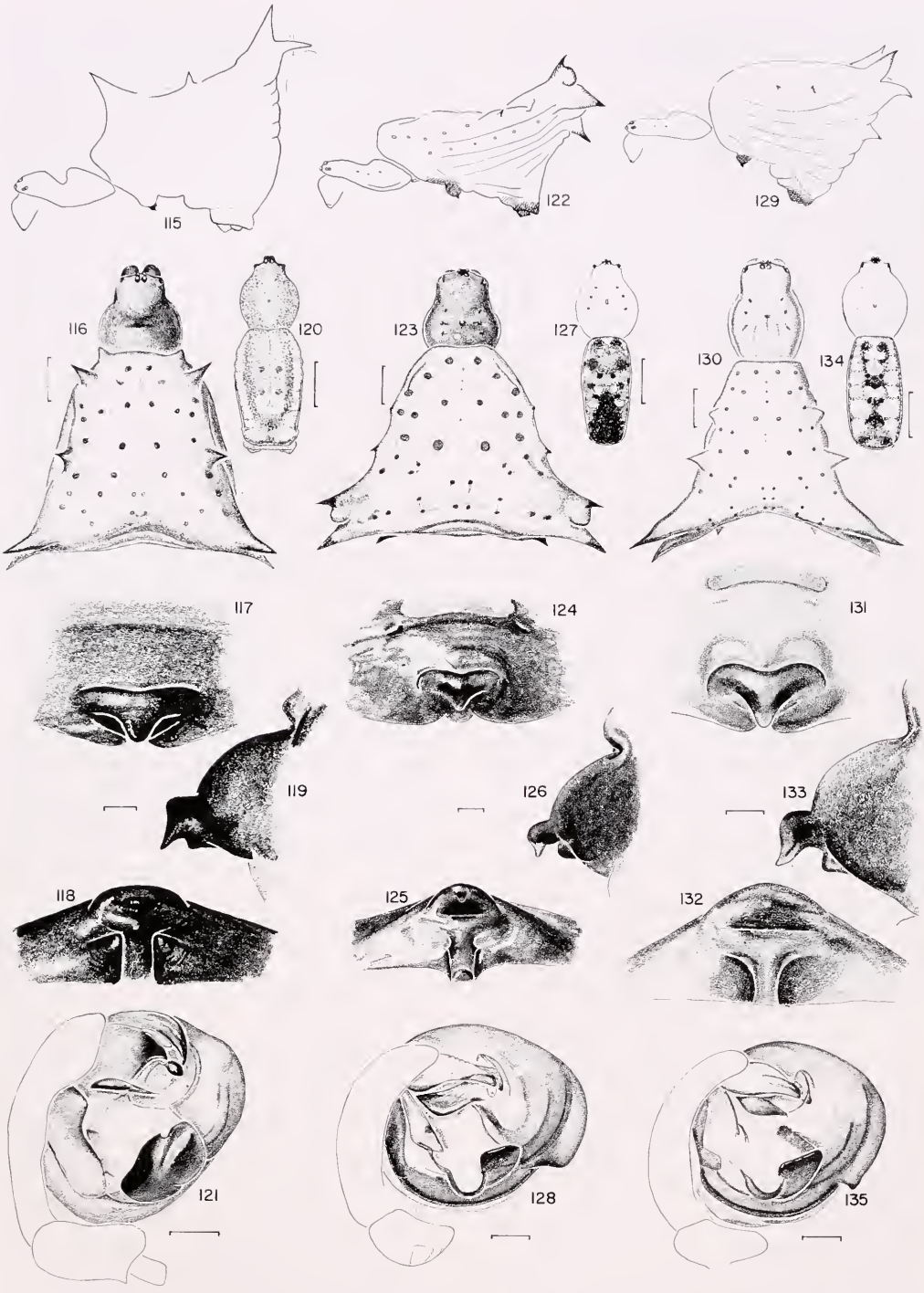
Figures 115–121. *Micrathena crassa* (Keyserling). 115–119. Female. 115. Lateral. 116. Dorsal. 117. Epigynum, ventral. 118. Epigynum, posterior. 119. Epigynum, lateral. 120, 121. Male. 120. Dorsal. 121. Left palpus, mesal.

Figures 122–128. *Micrathena digitata* (C. L. Koch). 122–126. Female. 122. Lateral. 123. Dorsal. 124. Epigynum, ventral. 125. Epigynum, posterior. 126. Epigynum, lateral. 127, 128. Male. 127. Dorsal. 128. Palpus, mesal.

Figures 129–135. *Micrathena furva* (Keyserling). 129–133. Female. 129. Lateral. 130. Dorsal. 131. Epigynum, ventral. 132. epigynum, posterior. 133. Epigynum, lateral. 134, 135. Male. 134. Dorsal. 135. Palpus, mesal.

Scale lines. 0.1 mm, except Figures 115, 116, 120, 122, 123, 127, 129, 130, 134, 1.0 mm.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Micrathena crassa (Keyserling)
Figures 115–121; Map 3

Acrosoma crassum Keyserling, 1863: 78, pl. 2, fig. 11, ♀. Female lectotype designated by Chickering, 1960, from Santa Fé de Bogota, Neu Granada [Bogotá, Colombia] (BMNH), examined; 1892: 19, pl. 1, fig. 15, ♀.

Micrathena xanthopyga Simon, 1895: 854, fig. 915, ♀. Immature lectotype and eight immature paralectotypes here designated from Venezuela (MNHN), examined. NEW SYNONYMY.

Micrathena tovarensis Simon, 1897b: 468. Two female syntypes from Colonia Tovar [1,802 m, Aragua], Venezuela (MNHN), examined. NEW SYNONYMY.

Micrathena aciculata Simon, 1897b: 469. Four juvenile syntypes from Colonia Tovar [1,802 m, Aragua], Venezuela in the MNHN, examined. NEW SYNONYMY.

Micrathena crassa:—Reimoser, 1917: 110, pl. 6, fig. 14, ♀. Roewer, 1942: 956. Bonnet, 1957: 2864. Chickering, 1960c: 71, figs. 21–25, ♀; 1961: 402, figs. 21–25, ♀.

Synonymy. Simon types of *M. tovarensis* are almost identical to Keyserling's specimens. The juveniles of *M. xanthopyga* and *M. aciculata* have the diagnostic deep groove across the carapace. The abdomen length of *M. aciculata* is 1.8 times the width, slightly wider behind than anteriorly, with eight spines. It comes from the same locality as *M. tovarensis.*

Description. Female. Carapace, sternum, legs orange-brown. Dorsum of abdomen white with spines, sclerotized areas dark brown, sides and posterior of dorsum gray. Carapace with a deep transverse groove between head and thorax; without rim or dimples; both head and thorax high (Fig. 115). Abdomen sometimes with small lobes anteriorly above carapace and four pairs of dorsal spines (Fig. 116). Total length, 6.0 mm. Carapace, 2.3 mm long, 1.9 mm wide. First femur, 2.0 mm; patella and tibia, 2.2 mm; metatarsus, 1.3 mm; tarsus, 0.7 mm. Second patella and tibia, 2.0 mm; third, 1.3 mm. Fourth femur, 2.5 mm; patella and tibia, 2.1 mm; metatarsus, 1.5 mm; tarsus, 0.7 mm.

Male from Utcuyacu, Peru. Carapace dark olive brown, darker on sides. Sternum dark brown. Coxae and legs whitish. Dorsum of abdomen with white pigment on sides, two gray longitudinal bands; sides whitish; venter black in middle; sides of black area with white pigment. Carapace with median thoracic depression; no rim or dimples (Fig. 120). First coxa with hook; second femur with groove. Total length, 4.4 mm. Carapace, 1.8 mm long, 1.3 mm wide. First femur, 1.4 mm; patella and tibia, 1.3 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm. Second patella and tibia, 1.2 mm; third, 0.6 mm. Fourth femur, 1.5 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 5.0 to 7.7 mm. The groove across the carapace is of variable depth. The anterolateral corners of the abdomen may form a blunt tooth.

Note. A single male has been collected with females at Utcuyacu, Peru. I am uncertain whether they belong together.

Diagnosis. This eight-spined species can be separated from others of the *kirbyi* group by the deep groove between the high head and high thorax (Fig. 115). The squared abdomen has the last two spines on a joined socket, the second pair smallest, in the middle of the side (Fig. 116).

Natural History. This is a montane forest species which has been collected in cloud forest at Monteverde, Costa Rica.

Distribution. Costa Rica to Argentina (Map 3).

Records. COSTA RICA: *Prov. Puntarenas.* Monteverde, 1,600 m, 19 July 1978, ♀ (C. L. Craig, P. Klass, MCZ), 1,525 m, 26 Nov. 1977, ♀ (C. L. Craig, MCZ), 1,600 m, 12 Nov. 1977, ♀ (C. L. Craig, MCZ). VENEZUELA: *Est. Mérida.* Mérida, June 1975, ♀ (MACN). COLOMBIA: "Río Negro," ♀ (NMW). *Dept. Cundinamarca.* Bogotá, ♀ (MCZ); Monteredondo, 1,200–2,000 m, 2♀ (MCZ). *Valle.* nr. Solidato, 1,600 m, 1,800 m, ♀ (MCZ); nr. Atuncela, 1,800 m, ♀ (MCZ). *Tolima.* 22 km W Fresno, ♀ (CAS). *Huila.* 12 km E of Sta. Leticia, 2,300 m, ♀ (MCZ). *Antioquia.* Medellín Valley, ♀ (MCZ). ECUADOR: *Prov. Pichincha.* Río Pilatón, ♀ (MCZ). *Tungu-*

rahua. Baños, ♀ (EPC); Río Topo, ♀ (EPC). *Pastaza*. Abitagua Mts., 1,200 m, 2♀ (AMNH). PERU: *Dept. Junín*. Utcuyacu, 1,600–2,200 m, 3♀, ♂ (AMNH, EPC). *Cuzco*. Chanchosmayo Basin, 2,150 m, ♀ (EPC). ARGENTINA: *Prov. Tucumán*. Pueblo Viejo, 19 Nov. 1959, 3♀ (Nuñoz, MACN).

Micrathena digitata (C. L. Koch) Figures 122–128; Map 3

Acrosoma digitatum C. L. Koch, 1839: 128, pl. 523, ♀. Female from Brazil (ZSM), destroyed.

Plectana bullata Walckenaer, 1841: 191. Female from Cayenne, French Guiana, lost. NEW SYNONYMY.

?*Plectana asciata* Walckenaer, 1841: 194. Female from Brazil, lost. NEW SYNONYMY.

Micrathena digitata:—Reimoser, 1917: 119, pl. 7, fig. 18, ♀. Roewer, 1942: 957. Bonnet, 1957: 2866. Chickering, 1960c: 75, figs. 33–37, ♀.

Micrathena hyatti Chickering, 1960c: 80, figs. 58–62, ♀. Female holotype from Joinville, Est. Santa Catarina, Brazil (BMNH), examined. NEW SYNONYMY.

Synonymy. Walckenaer described the lobed spines of *Plectana bullata*, otherwise present in very few species, and ten spines, but then indicated that the species has only eight spines. The locality, Cayenne, is an error. *Plectana asciata* has a hatchet-shaped spine and is probably this species. *Micrathena hyatti* is a female with a shrivelled, leathery abdomen.

Description. Female. Carapace, sternum dark brown. Legs brown. Dorsum of abdomen yellow-white with brown spines; venter dark brown. Carapace with three pairs of dimples, a median thoracic depression, high thorax, and indistinct rim in dorsal view. Abdomen rounded in front, with two small spines on each side, the anterior smaller; large posterolateral double spines on each side, the anterior of which is lobed behind; and a large pair of spines below (Figs. 122, 123). Total length, 7.0 mm. Carapace, 2.8 mm long, 2.6 mm wide. First femur, 2.3 mm; patella and tibia, 2.4 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm. Second patella and tibia, 2.3 mm; third, 1.3 mm. Fourth femur, 2.6 mm; patella and tibia, 2.2 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm.

Male. Carapace dark orange-brown, blackish on sides. Sternum blackish brown. Coxae dark orange; more distal leg articles dark brown. Dorsum of abdomen with paired white spots, black and brown patches; venter black. Carapace with three pairs of dimples and a distinct thoracic depression (Fig. 127). First coxa with hook; second femur with proximal groove. Total length, 3.8 mm. Carapace, 1.8 mm long, 1.4 mm wide. First femur, 1.3 mm; patella and tibia, 1.4 mm; metatarsus, 1.0 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.7 mm. Fourth femur, 1.4 mm; patella and tibia, 1.2 mm; metatarsus, 1.0 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 5.2 to 8.0 mm. The first pair of spines (on the side) may be very small or absent. Southern specimens seem to have a smaller lobe. Females may grade into *M. furva* in the south. Males of *M. digitata* have the abdomen slightly narrower behind than in front but are otherwise like those of *M. furva*.

Note. The male is matched to the female because it is the most common male *Micrathena* in the Rio de Janeiro area and is also similar to the male of *M. furva*.

Diagnosis. Females differ from those of *M. furva* by having a lobe or swelling on the posterodorsal spine (Figs. 122, 123), absent in *M. furva*. It is possible that these are northern specimens of *M. furva*. The male has a palpus like that of *M. furva* (Fig. 128). The only other species with a lobed spine, *M. stuebeli*, has a wider abdomen and anterior spines.

Natural History. *Micrathena digitata* is found in forested areas, very common in the vicinity of Rio de Janeiro.

Distribution. Southeastern Brazil (Map 3).

Records. BRAZIL: *Est. Pará*. Belém, July 1971, ♀ (T. McGrath, MCZ, ?error in locality). *Rio de Janeiro*. Rio de Janeiro and Tijuca Mts., very common ♀, ♂ (AMNH, FZRS, MCZ, NRS, ZMB); Nova

Friburgo, 4♀ (ZMSP); Teresópolis, Feb. 1963, ♀ (IBSP); Niterói, ♀ (MNRJ). *Minas Gerais.* Belo Horizonte, Nov. 1919, ♀ (Cornell Univ. Exped., CUC); Ouro Prêto, April 1954, ♀ (N. L. H. Krauss, AMNH). *São Paulo.* Boracéia, 3♀ (MZSP); Pilar do Sul, ♀ (MZSP). *Paraná.* Curitiba, ♀ (MNRJ, MZSP). *Santa Catarina.* Joinville, 5♀ (MNRJ).

Micrathena furva (Keyserling)
Figures 129–135; Map 3

Acrosoma furvum Keyserling, 1892: 7, pl. 1, fig. 4, ♂. Male holotype from Taquara, Rio Grande do Sul, Brazil (BMNH), examined.

Micrathena tucumana Simon, 1897a: 7. Female holotype from San Pablo, Tucumán, Argentina (MIZT), examined. Reimoser, 1917: 122. Roewer, 1942: 965. Bonnet, 1957: 2881. NEW SYNONYMY.

Micrathena pfannli Reimoser, 1917: 111, pl. 5, fig. 13, ♀. Female holotype from Territory Foncière [near Puerto Foncière, Concepción, 20 km N of Puerto Pinasco], Paraguay (NMW), examined. Roewer, 1942: 961. Bonnet, 1957: 2874. NEW SYNONYMY.

Micrathena furva:—Reimoser, 1917: 154. Roewer, 1942: 958. Bonnet, 1957: 2868. Chickering, 1960c: 78, figs. 46–49, ♂.

Synonymy. Micrathena tucumana is the female of *A. furvum.* Simon did not illustrate *M. tucumana,* thus Reimoser did not recognize it when he described the female again as *M. pfannli.*

Description. Female. Carapace light orange. Sternum dark orange. Legs orange. Dorsum of abdomen orange-white with sclerotized areas orange. Carapace with high thorax and narrow rim, three pairs of dimples and a median thoracic mark. Abdomen soft with eight to ten spines: none anteriorly, one or two lateral pairs, a pair of posterolateral double spines, and a pair of spines below (Figs. 129, 130). Total length, 6.7 mm. Carapace, 2.4 mm long, 1.9 mm wide. First femur, 2.2 mm; patella and tibia, 2.3 mm; metatarsus, 1.4 mm; tarsus, 0.8 mm. Second patella and tibia, 1.9 mm; third, 1.3 mm. Fourth femur, 2.4 mm; patella and tibia, 2.2 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm.

Male. Carapace dark orange. Sternum dark brown. Coxae light orange, more distal leg articles light orange. Dorsum of abdomen with black and white pattern (Fig. 134); venter black. Carapace with three indistinct pairs of dimples and a very distinct thoracic depression. First coxa with distal hook, second femur with proximal groove. Abdomen almost rectangular, truncate anteriorly, rounded behind (Fig. 134). Total length, 4.2 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 1.5 mm; patella and tibia, 1.5 mm; metatarsus, 1.0 mm. Second patella and tibia, 1.3 mm; third, 0.8 mm. Fourth femur, 1.7 mm; patella and tibia, 1.2 mm; metatarsus, 1.0 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 5.3 to 7.6 mm, males from 3.8 to 4.4 mm. In females the first pair of lateral spines may be absent or present as soft humps. One female lacked the last, the posterior pair. In males, the terminal apophysis and the folded conductor behind the tip of the embolus are longer in specimens from the northern part of the range.

Note. Several collections contain both males and females.

Diagnosis. Micrathena furva females differ from *M. digitata* only in lacking the lobe on the posterodorsal spine (Fig. 130). Perhaps *M. furva* are only southern specimens of *M. digitata.*

The male palp (Fig. 135) is most similar to that of *M. digitata.* Very few males were available; the only discernible difference from *digitata* is that the abdomen of *M. furva* male is as wide behind as anteriorly, while that of *digitata* is slightly narrower behind. I suspect that *M. furva* is the same species as *M. digitata.*

Distribution. Southern Brazil to Argentina (Map 3).

Records. BRAZIL: *Est. Santa Catarina.* Pinal, ♀ (AMNH); Blumenau, 2♀ (NMW). *Rio Grande do Sul.* São Francisco de Paula, 3♀, ♂ (FZRS); Vila Oliva [Caxias do Sul], 7♀ (FZRS); Canela, 5♀, ♂ (FZRS); Montenegro, ♂ (FZRS); Sierra Granada, ♀ (MNRJ); Iraí, ♂ (FZRS); Pôrto Alegre, ♀

(IBSP, MNRJ); Pelotas (MCZ). URUGUAY: *Dept. San José.* Playa Pascuae, ♀ (MHNM); Arazati, ♀ (MHNM). *Tacuarembó.* Arroyo Laureles, ♀ (MHNM). *Artigas.* Arroyo de la Invernada, 3♀ (MHNM); Arroyo Tres Cruces, 2♀ (MHNM). *Colonia.* Aroyo Sarandi, 10♀ (MHNM). *Canelones.* Isla Buchental, ♀ (MHNM). *Rivera.* Minas de Corrales, ♀ (MHNM). *Minas.* Quebrada de los Cuervos, ♀ (MHNM). *Salto.* Río Arapey, ♀ (MHNM). ARGENTINA: *Misiones Prov.* Eldorado, ♀, ♂ (AMNH); Santa Ana, ♀, ♂ (MACN); Punto 17 de Octobre, 3♀ (MACN); Parque Nacional Iguazú, 2♀ (MEG); Santa María, 15♀, 2♂ (MACN). Monteagudo, 65♀, 6♂ (MACN). *Tucumán.* Cadillal, ♀ (IMLT). *Buenos Aires.* Tigre, ♀ (MACN); Paraná de los Palmas, ♀♀ (MACN, MEG); Punta Lara, ♀ (MULP, MACN); Isla Martin García 2♀ (MEG), 5♀ (MACN).

Micrathena fidelis (Banks)
Figures 136–143; Map 3

Acrosoma fidelis Banks, 1909a: 212. Female holotype from Tablazo [Cerro Tablazo], Costa Rica (MCZ), examined.

Micrathena cala Chamberlin, 1916: 261, pl. 20, fig. 6, juv. Immature female from San Miguel, 6,000 ft. [2,000 m], Ayacucho, Peru (MCZ), examined. NEW SYNONYMY.

Micrathena fidelis:—Reimoser, 1917. Chickering, 1961: 411: 46–49, ♀. Roewer, 1942: 954. Bonnet, 1957: 2867.

Synonymy. The immature type of *M. cala* (Fig. 141) has the same number and shape of abdominal spines and has the diagonistic black area between the posterior spines. Also, it was found in the mountains, like other specimens of *M. fidelis.*

Description. Female holotype. Carapace orange-brown. Sternum orange. Legs orange-brown. Dorsum of abdomen white, posterior black between third and fourth pair of spines; sides black with several square white patches dorsally (Fig. 136); venter black with one white patch on each side of genital area and two white spots on each side of spinnerets. Carapace large with narrow rim, distinct thoracic mark, but no dimples; thorax low (Fig. 136). Abdomen trapezoidal, widest behind, with eight spines; spines soft with black tips (Figs. 136, 137). Total length, 6.1 mm. Carapace, 2.3 mm long, 1.9 mm wide. First femur, 2.3 mm; patella and tibia, 2.3 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm. Second patella and tibia, 2.2 mm; third, 1.3 mm. Fourth femur, 2.4 mm; patella and tibia, 2.2 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm.

Male. Carapace yellow-brown, darker on sides. Sternum black, coxae yellow. Legs yellow, distally darker. Dorsum of abdomen maculated black and white; venter black, with a white spot on posterior end. Carapace without dimples, thoracic depression distinct (Fig. 142). Coxal hook present. Total length, 4.8 mm. Carapace, 2.0 mm long, 1.4 mm wide. First femur, 1.6 mm; patella and tibia, 1.5 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.7 mm. Fourth femur, 1.6 mm; patella and tibia, 1.3 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 4.8 to 6.4 mm. The coloration of some South American specimens is variable.

Note. A male has been collected with a female at Saladito, Colombia.

Diagnosis. Micrathena fidelis can be separated from *M. agriliformis* by body proportions and spines, and by the epigynum having a straight transverse bar with lobe (Fig. 138). In posterior view there are two transverse lips (Fig. 139).

The male differs from *M. pupa* by having a shorter embolus (Fig. 143). It differs from *M. agriliformis* by the arched embolus passing below the distal edge of the semitransparent terminal apophysis. The sclerotized rim of the median apophysis is relatively larger than that of *M. agriliformis* (Fig. 143).

Distribution. Costa Rica to Argentina, in mountains (Map 3).

Records. COSTA RICA: *San José Prov.*

Cerro de Escazú, 2,400 m, Dec. 1981, ♀ (W. Eberhard, MCZ); Pico Blanco, above Escazú, 2,000 m, March 1983, ♀ (W. Eberhard, MCZ); Bajo la Hondura, 28 March 1981, ♀ (V. Zelédon, ZMCR). *Alajuela.* Vara Blanca, ♀ (ZMCR). PANAMA: *Chiriquí Prov.* Cerro Punta, June 1962, ♀ (R. Zweifel, AMNH). COLOMBIA: *Dept. Magdalena.* Sierra Nevada de Santa Marta: 9–12 Feb. 1929, ♀ (P. J. Darlington, MCZ); San Pedro, 1,400 m, 17 Feb. 1974, ♂ (J. Kochalka, JAK); Serachui, 1,600 m, 4 March 1974, ♀ (J. Kochalka, JAK); Serra Nueva Granada, 1,600 m, April 1975, 2♀ (J. Kochalka, JAK). *Valle.* above Felicia, 1,800 m, ♀ (W. Eberhard, MCZ); Arriba de Saladito, 1,800 m, 24 Dec. 1973, ♀, ♂ (W. Eberhard, MCZ). BOLIVIA: *Dept. La Paz.* Chulumani, 1,700 m, Yungas, July 1955, ♂ (L. Peña, MCZ). ARGENTINA: *Salta Prov.* Calilegua, Valle Grande, Nov. 1968, ♀ (M. E. Galiano, MEG).

Micrathena gaujoni Simon
Figures 144–148; Map 3

Micrathena gaujoni Simon, 1897b: 466. Five female syntypes from Loja, Ecuador (no. 7832, MNHN), examined and labeled.

Description. Female syntype. Carapace brown, with a dark brown band on each side of thorax; rim light. Sternum, coxae light brown; distal leg articles brown. Dorsum of abdomen gray with some white marks; spines usually orange to red-brown, tips black; sides with dark dorsoventral streaks and row of white spots; venter black between epigynum and spinnerets. Carapace with a narrow rim, distinct thoracic depression and high thorax. Abdomen longer than wide, with a pair of spines one third from anterior end and three pairs of posterior spines (Figs. 144, 145). Total length, 8.3 mm. Carapace, 2.4 mm long, 1.8 mm wide. First femur, 2.7 mm; patella and tibia, 2.7 mm; metatarsus, 1.8 mm; tarsus, 0.8 mm. Second patella and tibia, 2.5 mm; third, 1.4 mm. Fourth femur, 3.0 mm; patella and tibia, 2.6 mm; metatarsus, 1.9 mm; tarsus, 0.8 mm.

Variation. Females vary in total length from 8.0 to 8.3 mm. The epigynum (Figs. 146–148) is quite variable in structure, perhaps due to differing amounts of sclerotization. The illustrations were made from specimens coming from SW of Mocoa, Colombia.

Note. The male is unknown.

Diagnosis. This species differs from *M. fissispina* by being smaller in size and having a sclerotized cheek on each side of the lobe of the epigynum (Fig. 146).

Distribution. Southern Colombia to Ecuador (Map 3).

Records. COLOMBIA: *Dept. Putumayo.* 40 km SW Mocoa, 3 March 1955, ♀ (E. I. Schlinger, E. S. Ross, CAS). ECUADOR: Loja to Zamora, 1,800–2,200 m, 24–25 Aug. 1977, ♀ (L. Peña, AMNH).

Micrathena fissispina (C. L. Koch)
Figures 149–155; Map 3

Acrosoma fissispina C. L. Koch, 1836: 54, fig. 208. Female from Brazil, lost.

Micrathena fissispina:—Simon, 1895: 852, fig. 903, ♀. Reimoser, 1917: 120, pl. 7, fig. 20, ♀. Roewer, 1942: 957. Bonnet, 1957: 2867.

Micrathena tigris Mello-Leitão, 1932: 87, fig. 5, ♀. Female type from Tapera, Pernambuco, Brazil (MNRJ), lost. NEW SYNONYMY.

Synonymy. Several museums (ZMB, MNHN, PAN) have old specimens labeled

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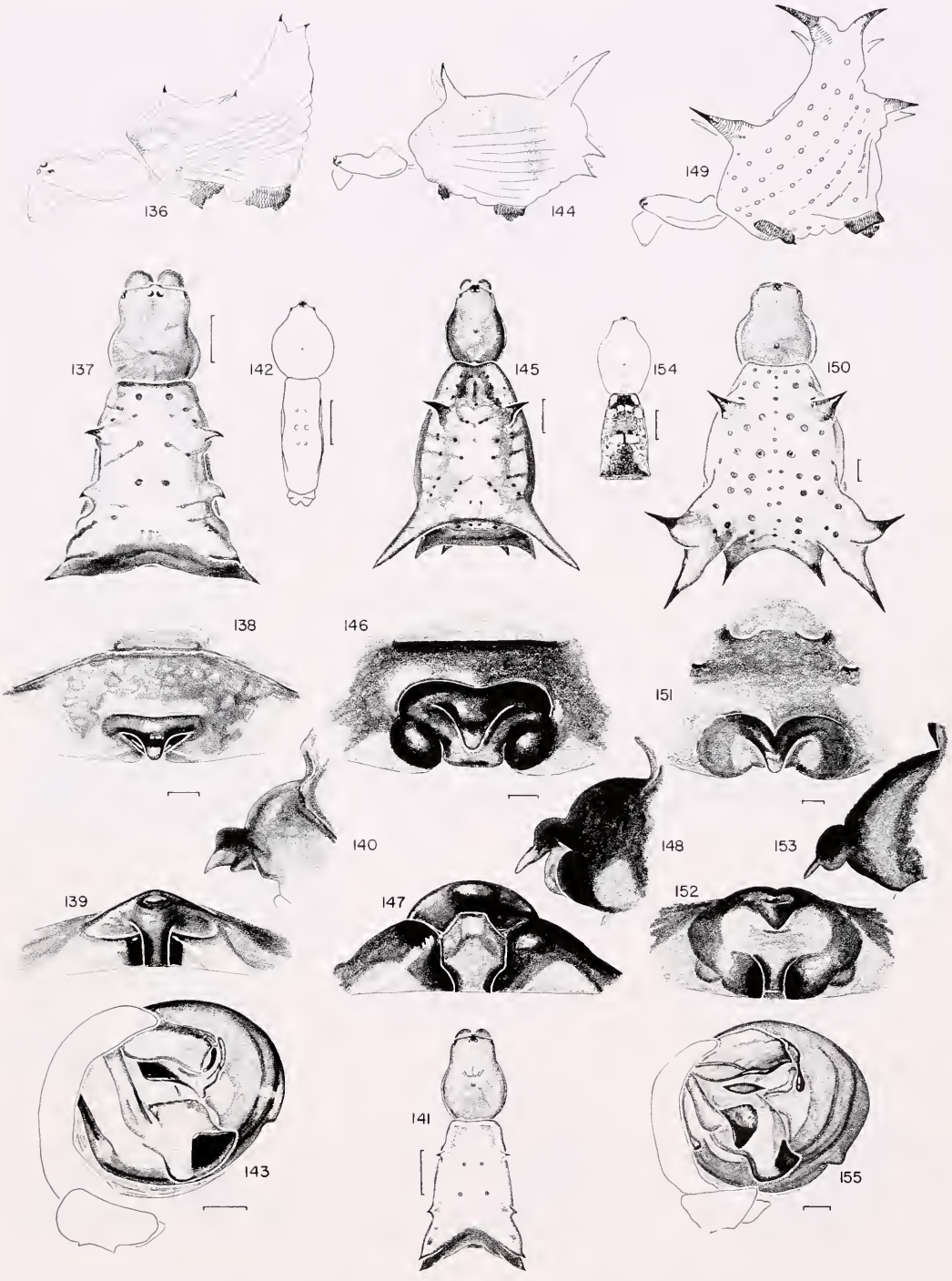
Figures 136–143. *Micrathena fidelis* (Banks). 136–140. Female. 136. Lateral. 137. Dorsal. 138. Epigynum, ventral. 139. Epigynum, posterior. 140. Epigynum, lateral. 141. Juvenile, dorsal. 142, 143. Male. 142. Dorsal. 143. Left palpus, mesal.

Figures 144–148. *Micrathena gaujoni* Simon, female. 144. Lateral. 145. Dorsal. 146. Epigynum, ventral. 147. Epigynum, posterior. 148. Epigynum, lateral.

Figures 149–155. *Micrathena fissispina* (C. L. Koch). 149–153. Female. 149. Lateral. 150. Dorsal. 151. Epigynum, ventral. 152. Epigynum, posterior. 153. Epigynum, lateral. 154, 155. Male. 154. Dorsal. 155. Palpus, mesal.

Scale lines. 0.1 mm, except Figures 136, 137, 141, 142, 144, 145, 149, 150, 154, 1.0 mm.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fissispina; all are this species. The type vial of *M. tigris* contained the type of *M. conspicua* (=*Chaetacis picta*); the illustration and description appear to be this species.

Description. Female. Carapace, sternum, legs orange-brown; rim of carapace white. Dorsum of abdomen white with tips of spines black; sclerotized areas orange-brown; sides and venter black with white patches. Carapace with thoracic depression and high thorax; lacking dimples. Abdomen with eight spines, of which the second and third pairs have a common socket (Figs. 149, 150). Total length, 12.0 mm. Carapace, 4.6 mm long, 3.8 mm wide. First femur, 5.2 mm; patella and tibia, 5.6 mm; metatarsus, 4.1 mm; tarsus, 1.4 mm. Second patella and tibia, 4.9 mm; third, 2.8 mm. Fourth femur, 6.2 mm; patella and tibia, 4.9 mm; metatarsus, 4.0 mm; tarsus, 1.4 mm.

Male. Carapace dark orange. Sternum, labium and endites black. Legs orange. Dorsum of abdomen white and black, venter black. Carapace low, with distinct thoracic depression; no dimples. First coxa with hook. Abdomen rectangular, slightly wider posteriorly (Fig. 154). Total length, 5.9 mm. Carapace, 2.9 mm long, 1.9 mm wide. First femur, 2.6 mm; patella and tibia, 2.5 mm; metatarsus, 1.9 mm; tarsus, 0.9 mm. Second patella and tibia, 1.9 mm; third, 1.2 mm. Fourth femur, 2.8 mm; patella and tibia, 2.1 mm; metatarsus, 1.9 mm; tarsus, 0.7 mm.

Variation. Females vary in total length from 8.7 to 13.0 mm.

Note. A collection from Itamarajá, Est. Bahia had a male collected with two females.

Diagnosis. Micrathena fissispina is larger than *gaujoni* and lacks the cheeks on each side of the epigynum lobe (Fig. 151). The male differs from other species by the sclerotized drop-shaped structure below the tip of the conductor and by the sclerite at the base of the median apophysis (Fig. 155).

Distribution. Eastern South America (Map 3).

Records. FRENCH GUYANA: Cayenne (PAN). BRAZIL: *Est. Pará.* Ilha do Marajó, June 1954, ♀ (W. Forster and O. Schindler, ZSM). *Bahia.* Salvador, ♀ (ZMB, ZMK); Itamarajá, 9 Dec. 1977, ♀, 7 Aug. 1978, 2♀, ♂ (J. Santos, FZRS); Mucurí, 14 Oct. 1979, ♀ (A. C. Niella, FZRS); Iguassú, 2 July 1926, ♀, 30 June 1924, ♀, 4 Aug. 1924, 3♂ (A. Roman, NRS); Camaçari, 14 Oct. 1978, ♀ (J. S. Santos, FZRS); Ilhéus, Jan. 1964, ♀, ♂ (Papavero, MZSP). *Rio de Janeiro.* Rio de Janeiro, ♀ (ZMK). *São Paulo.* Bertioga, 2 Jan. 1962, 3♀; 21 Nov. 1961, ♀, 22 Dec. 1961, 2♀ (A. Barroso, MZSP); Praia Itaguaré, 3 Feb. 1964, 2♀ (MZSP). *Santa Catarina.* 5♀ (MCZ); Blumenau, 15 Nov. 1886, 6♀ (NMW).

Micrathena raimondi (Taczanowski)
Figures 156–163; Map 3

Acrosoma raimondii Taczanowski, 1879: 118. Female holotype from Montana de Nancho, 3,600 pieds d'altitude [near Nanchoc, Cajamarca, 1,200 m], Peru (PAN), examined.

Micrathena raimondi:—Roewer, 1942: 962. Bonnet, 1957: 2875.

Note. The holotype has the scape of the epigynum broken off.

Description. Female from Cajamarca, Peru. Carapace brown, eye region and thorax light, sides of thorax dark, rim

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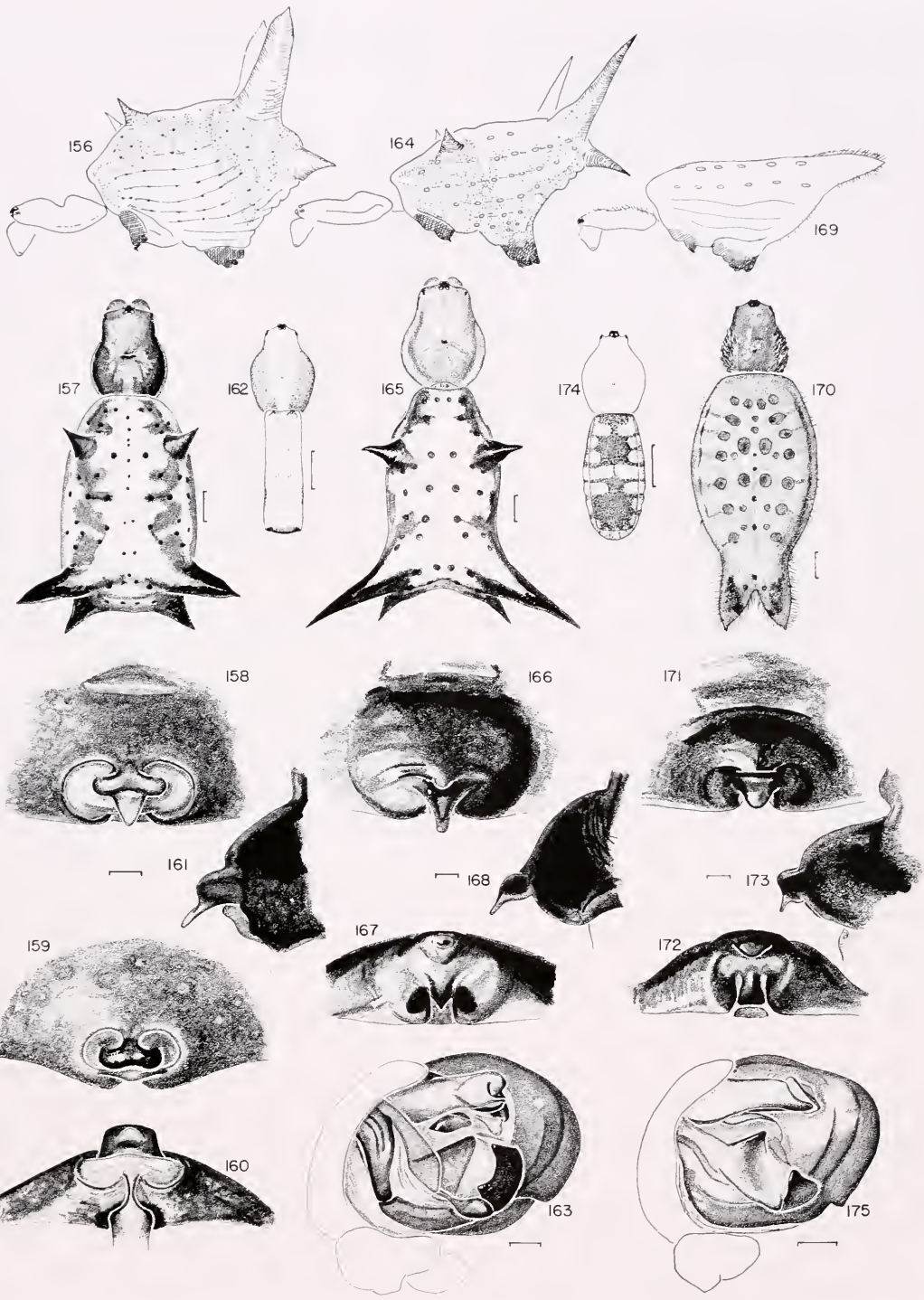
Figures 156–163. *Micrathena raimondi* (Taczanowski). 156–161. Female. 156. Lateral. 157. Dorsal. 158, 159. Epigynum, ventral. 159. Scape tip torn off. 160. Epigynum, posterior. 161. Epigynum, lateral. 162–163. Male. 162. Dorsal. 163. Left palpus, mesal.

Figures 164–168. *Micrathena miles* Simon, female. 164. Lateral. 165. Dorsal. 166. Epigynum, ventral. 167. Epigynum, posterior. 168. Epigynum, lateral.

Figures 169–175. *Micrathena furcula* (O. P.-Cambridge). 169–173. Female. 169. Lateral. 170. Dorsal. 171. Epigynum, ventral. 172. Epigynum, posterior. 173. Epigynum, lateral. 174, 175. Male. 174. Dorsal. 175. Palpus, mesal.

Scale lines. 0.1 mm, except Figures 156, 157, 162, 164, 165, 169, 170, 174, 1.0 mm.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lightest. Sternum dark brown. Coxae and distal articles of legs brown. Dorsum of abdomen with a black longitudinal band on each side between spines (Fig. 157); sides with white spots; venter with white spots on side, but none in middle between epigynum and spinnerets. Carapace with a deep transverse groove and a narrow rim; no dimples (Fig. 157). Abdomen with three pairs of spines, middle one largest (Fig. 157). Total length, 10.4 mm. Carapace, 3.0 mm long, 2.4 mm wide. First femur, 3.2 mm; patella and tibia, 3.5 mm; metatarsus, 2.3 mm; tarsus, 0.9 mm. Second patella and tibia, 3.0 mm; third, 1.9 mm. Fourth femur, 3.8 mm; patella and tibia, 3.4 mm; metatarsus, 2.6 mm; tarsus, 1.0 mm.

Male. Carapace orange, sides brown. Sternum dark brown. Coxae orange, distal articles of legs brown; first legs darkest, third lightest. Dorsum of abdomen speckled white with some dark marks on corners; venter black. First coxa with hook; second femur with proximal groove. Abdomen rectangular (Fig. 162). Total length, 5.6 mm. Carapace, 2.6 mm long, 1.1 mm wide. First femur, 2.2 mm; patella and tibia, 2.3 mm; metatarsus, 1.7 mm; tarsus, 0.8 mm. Second patella and tibia, 2.0 mm; third, 1.2 mm. Fourth femur, 2.6 mm; patella and tibia, 2.2 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm.

Variation. Females vary in total length from 6.3 to 10.4 mm, males from 5.6 to 5.9 mm. The second pair of spines is variable in length.

Note. Three collections contained females together with males.

Diagnosis. Females of this species are distinguished from the similar *M. miles* by the dorsal markings, the dark patch between the first and second pair of abdominal spines on each side (Fig. 157), by the narrower carapace rim (Fig. 157), by the smaller size and the round frame on each side of the epigynum (Fig. 158).

The male differs from others of this species group by the shallow notch of the tip of the median apophysis and by the shape of the tip of the terminal apophysis and conductor (Fig. 163).

Distribution. Ecuador and Peru (Map 3).

Records. ECUADOR: *Prov. Pichincha.* Tandapi, 1,300–1,500 m, 15–20 May 1965, 13♀, 2♂ (L. Peña, MCZ); Río Pilatón, 7♀ (G. W. Prescott, MCZ). Río Yocuchoqui, W slope of Andes, 2♀, ♂ (MCZ). PERU: *Dept. Cajamarca.* W of Porcullo [?], 15–19 May 1967, 9♀, ♂ (A. F. Archer and S. Risco, AMNH).

Micrathena miles Simon
Figures 164–168; Map 3

Micrathena miles Simon, 1895: 852, fig. 907; 1896: 468. Female syntypes from Fonte Bôa and Tefé, Amazon, Brazil (no. 1172, MNHN), examined. Roewer, 1942: 960. Bonnet, 1957: 2872.

Micrathena cuminamensis Mello-Leitão, 1930: 62, fig. 16, ♀. Female from Rio Cuminá [Rio Paru de Ooste, Est. Pará], Brazil (MNRJ), lost. NEW SYNONYMY.

Micrathena miles nigra di Caporiacco, 1948: 667. Immature from Tumatumari, Guyana (ZMF), examined. NEW SYNONYMY.

Synonymy. The illustration of *M. cuminamensis* appears to be this species, although the sternum is described as being yellow. The type is lost, but there are two other specimens from Rio Cuminá in the MNRJ labeled *M. miles.* Di Caporiacco's specimen, an immature, appears also to be this species.

Description. Female from Rio Purus, Brazil. Carapace orange, rims light orange, sternum black. Coxae orange, distal leg articles orange-black. Dorsum of abdomen yellow-white, rimmed by black; sides black with dorsoventral rows of white spots; venter black with small paired black spots (Figs. 164–165). Carapace with distinct thoracic depression, wide rim and thorax higher than head; no dimples. Anterior and venter of femora have tubercles tipped by short, sharp setae. Abdomen longer than wide, with six spines (Figs. 164, 165). Total length, 11.5 mm. Carapace, 4.0 mm long, 3.2 mm wide. First femur, 5.2 mm; patella and tibia, 4.8 mm;

metatarsus, 3.7 mm; tarsus, 1.3 mm. Second patella and tibia, 2.7 mm; third, 2.3 mm. Fourth femur, 6.4 mm; patella and tibia, 5.0 mm; metatarsus, 4.8 mm; tarsus, 1.4 mm.

Variation. Females vary in total length from 11.5 to 13.2 mm.

Note. The male is unknown.

Diagnosis. This species differs from *Micrathena raimondi* by lacking a frame on each side of the transverse bar and lobe of the epigynum (Fig. 166). It differs from *M. kirbyi* by lacking anterior spines overhanging the carapace (Fig. 165).

Distribution. Amazon area (Map 3).

Records. BRAZIL: *Est. Pará.* Rio Tapajós, 25 Aug. 1978, 2♀ (Lacey, INPA); Rio Cuminá, 2♀ (no. 14085, MNRJ). *Acre.* Rio Purus, W of Sena Madureira, 5 Sept. 1973, ♀ (B. Patterson, MCZ). PERU: *Dept. Loreto.* Iquitos, May 1920, ♀ (H. S. Parrish, MCZ).

Micrathena furcula (O. P.-Cambridge)
Plate 1; Figures 169–175; Map 4

Acrosoma furcula O. P.-Cambridge, 1890: 60, pl. 8, fig. 11, ♀. Female syntypes from Dolores, Menché on the river Usumacinta between Dolores and Chapallal [Dept. Petén], Guatemala (BMNH), lost. Keyserling, 1892: 17, pl. 1, fig. 13, ♀.

?*Micrathena pubescens* Simon, 1895: 854, figs. 917, 918. Juvenile female lectotype here designated from Mato Grosso (MNHN), examined and labeled. NEW DOUBTFUL SYNONYMY.

Micrathena furcula:—F. P.-Cambridge, 1904: 539, pl. 51, fig. 25, ♀. Reimoser, 1917: 89. Roewer, 1942: 958. Bonnet, 1957: 2368. Chickering, 1961: 416, figs. 60–66, ♀, ♂.

Synonymy. The immature specimen of *M. pubescens* was in a vial with an adult male of *M. plana* and some other immature specimens. Only finding an adult female from Mato Grosso will ascertain that there is only one species. Perhaps there is an error in the locality of Simon's specimen.

Description. Female from Panama. Carapace dark red-brown. Sternum black-brown. Legs brown. Abdomen brownish white on dorsum, sclerites brown; a black patch on each fork (Fig. 170), and sometimes median dark mark resembling that of male (Fig. 174); venter black; fork with a lighter band spreading posterolaterally from spinnerets. Carapace covered with down; with a round thoracic mark; no dimples or rim. Abdomen is forked, without spines (Fig. 170). Total length, 11.2 mm. Carapace, 3.2 mm long, 2.4 mm wide. First femur, 2.7 mm; patella and tibia, 2.7 mm; metatarsus, 1.8 mm; tarsus, 0.8 mm. Second patella and tibia, 2.2 mm; third, 1.4 mm. Fourth femur, 3.3 mm; patella and tibia, 2.7 mm; metatarsus, 1.9 mm; tarsus, 0.7 mm.

Male from Panama. Carapace, sternum dark brown, legs brown. Dorsum of abdomen with black and white marks (Fig. 174), sclerotized shield brown; venter black. Carapace slightly pubescent on sides with a median mark; no dimples or rim. Small coxal hook present; small groove on second femur. First and second legs strong, with macrosetae on femur and tibia. Total length, 4.8 mm. Carapace, 2.2 mm long, 1.5 mm wide. First femur, 1.6 mm; patella and tibia, 1.7 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm. Second patella and tibia, 1.4 mm; third, 0.9 mm. Fourth femur, 1.9 mm; patella and tibia, 1.4 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm.

Variation. Females vary in total length from 8.4 to 11.0 mm, males from 4.7 to 4.8 mm.

Note. The male and female were matched by Chickering because immature males are strongly pubescent and otherwise look like the adult male. The structure of the male palpus (Fig. 175) indicates a close relationship to *M. mitrata* and *M. bimucronata.*

Diagnosis. The pubescence on the carapace and the forked abdomen (Figs. 169, 170) distinguish females from other species. The male palp is similar to that of species related to *M. bimucronata* with a sclerotized tooth at the base of the median apophysis, and separated from related species by the shape of the terminal apophysis and conductor (Fig. 175).

Natural History. Specimens have been

taken from *Sceliphron* wasp nests in Costa Rica.

Distribution. Guatemala to southern Colombia (perhaps Brazil) (Map 4).

Records. COSTA RICA: *Prov. Heredia.* La Selva, nr. Puerto Viejo, 29 June 1979, 4 July 1979, 2♀ (J. Coddington, MCZ). *Puntarenas.* Corcovado Natl. Park, Sirena Sta., 31 Aug. 1982, ♀♀ (R. Matthews, MCZ). PANAMA: *Prov. Panamá.* Barro Colorado Island, Gatún Lake, many collections (AMNH, CUC, MCZ). COLOMBIA: *Dept. Valle.* Baja Calima, nr. Puerto Patiña, 10–13 July 1981, ♀ (B. Opell, MCZ).

Micrathena bimucronata (O. P.-Cambridge) Figures 176–182; Map 4

Acrosoma bimucronatum O. P.-Cambridge, 1899: 302, pl. 36, fig. 14, ♀. Twelve female syntypes from Cahabón, seven from Chisec and nine from Menché, Guatemala (BMNH), examined.

Micrathena bimucronata:—F. P.-Cambridge, 1904: 538, pl. 51, fig. 23, ♀. Reimoser, 1917: 124. Roewer, 1942: 954. Bonnet, 1957: 2863. Chickering, 1961: 936, figs. 1–5, ♀.

Description. Female from Costa Rica. Carapace brown, head region orange; rim of thorax narrow and light. Sternum dark brown. Coxae and legs lighter orange. Dorsum of abdomen white with posterior spines having some black pigment; sides with indistinct vertical black bands; venter white with transverse black band through middle and more bands posteriorly connecting with vertical bands. Carapace high with U-shaped thoracic depression and two pairs of dimples (Fig. 177). Abdomen with two posterior spines and minute denticles on sides of posterior half (Figs. 176, 177). Total length, 6.0 mm. Carapace, 2.0 mm long, 1.9 mm wide. First femur, 2.0 mm; patella and tibia, 2.1 mm; metatarsus, 1.3 mm; tarsus, 0.5 mm. Second patella and tibia, 1.9 mm; third, 1.2 mm. Fourth femur, 2.2 mm; patella and tibia, 2.0 mm; metatarsus, 1.4 mm; tarsus, 0.8 mm.

Male from Costa Rica. Carapace, legs orange. Sternum dusky orange. Dorsum of abdomen with white patches and indistinct black marks; venter blackish. Carapace with distinct thoracic depression. First coxa with small hook, second femur with groove. Abdomen slightly longer than wide, rounded behind (Fig. 181). Total length, 3.5 mm. Carapace, 1.7 mm long, 1.3 mm wide. First femur, 1.4 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm. Second patella and tibia, 1.1 mm; third, 0.6 mm. Fourth femur, 1.4 mm; patella and tibia, 1.1 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 4.5 to 6.2 mm, males from 3.3 to 3.6 mm. Posterior lateral spines of many specimens are longer than those illustrated (Fig. 177).

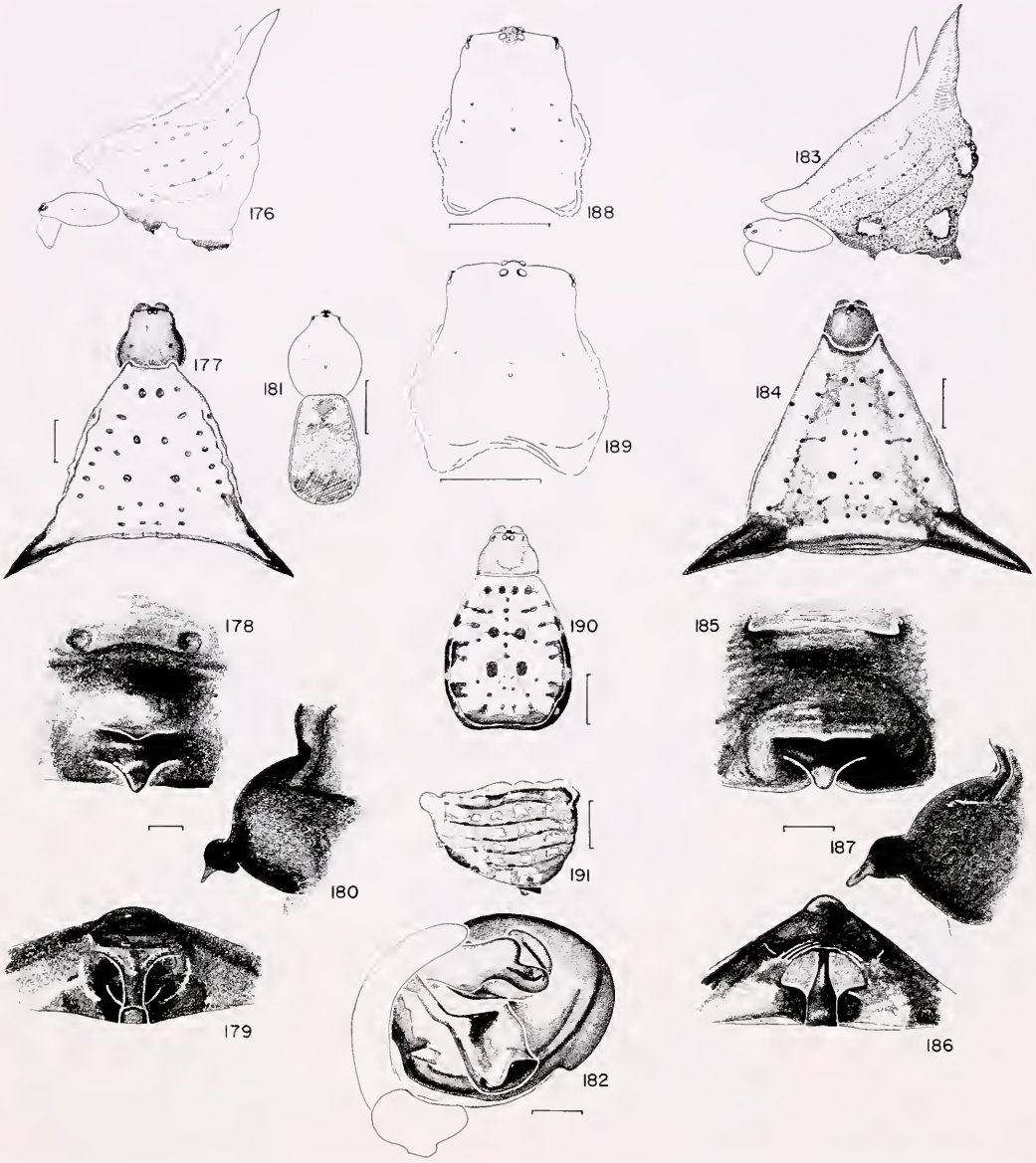
Note. Males and females were matched from a collection by W. Peck of females with two males from Turrialba, Costa Rica.

Diagnosis. The coloring of *M. bimucronata* is quite different from that of *M. rufopunctata* (Fig. 177), and the epigynum has a wider septum in posterior view (Fig. 179). The terminal apophysis covering the embolus has lobes differently shaped from those of *M. mitrata,* and the conductor is more distant from the tip of the cymbium (Fig. 182).

Natural History. Webs were found in low vegetation and dense jungle in Costa Rica.

Distribution. Chiapas to western Panama (Map 4).

Records. MEXICO: *Est. Chiapas.* Lacandone forest, 40 km NE of Ocosingo, 4 March 1945, ♀ (T. C. Schneirla, AMNH). HONDURAS: *Dept. Atlántida.* Lancetilla, 29 July 1929, ♂ (A. M. Chickering, MCZ). COSTA RICA: *Heredia Prov.* La Selva, Puerto Viejo, Dec. 1980, 2♂ (W. Eberhard, MCZ), ♀ (L. Higgins, MCZ); nr. La Virgen, 8 Aug. 1978, ♀ (A. M. Young, MPM). *Cartago.* Turrialba, 10–17 April 1944, ♀, ♂, 15–30 May 1944, ♀ (F. Schrader, AMNH), March 1967, 4♀, 2♂ (W. Peck, EPC). *Limón.* Siquirres, 20–23 May 1944, ♀ (F. Schrader, AMNH); Sixola River, ♀ (G. C. Wheeler, MCZ); Tortuguero Natl. Park, low wet coast forest, 25 Sept. 1976, ♀ (C. L. Craig, MCZ); Tortuguero,



Figures 176–182. *Micrathena bimucronata* (O. P.-Cambridge). 176–180. Female. 176. Lateral. 177. Dorsal. 178. Epigynum, ventral. 179. Epigynum, posterior. 180. Epigynum, lateral. 181, 182. Male. 181. Dorsal. 182. Left palpus, mesal.

Figures 183–187. *Micrathena rufopunctata* (Butler), female. 183. Lateral. 184. Dorsal. 185. Epigynum, ventral. 186. Epigynum, posterior. 187. Epigynum, lateral.

Figure 188. *Micrathena mitrata* (Hentz), female carapace. Figures 189–191. *Micrathena saccata* (C. L. Koch). 189. Female carapace. 190, 191. Immature male. 190. Dorsal. 191. Abdomen, lateral.

Scale lines. 0.1 mm, except Figures 176, 177, 181, 183, 184, 188–191, 1.0 mm.

Feb. 1931, 2♀ (Nevermann, NMW); Waldeck Farm, 45 km N of Limón, 11 Aug. 1930, ♀ (E. Reimoser, NMW). *Guanacaste*. Carillo, ♀ (MCZ). *San José*. San José, ♀ (MCZ). PANAMA: *Prov. Bocas del Toro*. 5♀, 11 imm. (F. R. Swift, CUC).

Micrathena rufopunctata (Butler)
Figures 183–187; Map 4

Acrosoma rubrocinctum Butler, 1873: 423. Female holotype from Brazil (BMNH), examined. NEW SYNONYMY.

Acrosoma rufopunctatum Butler, 1873: 423. Female holotype from Jamaica (BMNH), examined.

Micrathena rufopunctata:—Reimoser, 1917: 152. Roewer, 1942: 962. Bonnet, 1957: 2875. Chickering, 1964: 277, figs. 64–67, ♀.

Micrathena rubrocincta:—Reimoser, 1917: 153. Roewer, 1942: 962. Bonnet, 1957: 2875.

Note. No other specimens of *M. rubrocincta* have been found from Brazil. The type specimen is another of *M. rufopunctata*, with an erroneous locality. Even though the name *rubrocincta* has line priority over *rufopunctata*, I use the latter because it has the correct locality and there are literature references.

The types had been pinned and are in poor physical condition. They are now in alcohol.

Description. Female. Carapace, sternum, legs dark brown. Dorsum of abdomen with orange band on each side, a transverse posterior orange band enclosing subtriangular area of white pigment overlain by black all around, with white only in center (Fig. 184); posterolateral spines dark brown; venter black with three pairs of discreet white patches, probably red in living specimens (Fig. 183). Carapace fairly high with circular thoracic depression, sometimes with an indistinct pair of dimples (Fig. 183). Abdomen subtriangular with a pair of anterior blunt humps overhanging carapace and very strong, large posterolateral spines. Total length, 5.2 mm. Carapace, 1.9 mm long, 1.7 mm wide. First femur, 1.7 mm; patella and tibia, 1.7 mm; metatarsus, 1.1 mm; tarsus, 0.6 mm. Second patella and tibia, 1.5 mm; third, 1.0 mm. Fourth femur, 1.9 mm; patella and tibia, 1.5 mm; metatarsus, 1.2 mm; tarsus, 0.5 mm.

Note. The male is unknown.

Diagnosis. The striking coloration of *M. rufopunctata* separates the species from the similar *M. bimucronata*.

Distribution. Jamaica, uncommon (Map 4).

Records. JAMAICA. *St. Ann's Parish*: Mt. Diabolo Forest Reserve, 29 June 1960, 3♀ (T. H. Farr, AMNH), 19 Aug. 1960, ♀ (T. H. Farr, IJK). *Portland*. Ecclesdown, 21 June 1961, ♀ (T. H. Farr, IJK). *St. Catherine*. Guanaboa Vale, 13 Nov. 1960, ♀ (T. H. Farr, IJK). *Manchester*. Christiana, 11 June 1959, ♀ (T. H. Farr, IJK). *Trelawny*. NW of Quickstep, 17 March 1962, ♀ (J. Poulter, IJK).

Micrathena mitrata (Hentz)
Figures 188, 192–198; Map 4

Epeira mitrata Hentz, 1850: 22, pl. 3, fig. 11, ♀. Syntypes from North Carolina and Alabama, destroyed.

? *Micrathena peruana* Taczanowski, 1879: 116, pl. 1, fig. 32, ♀. Female holotype from Amable María [Junín, Prov. Tarma], Peru (PAN), examined. NEW SYNONYMY.

Micrathena patruelis:—F. P.-Cambridge, 1904, 583. Roewer, 1942: 960. Bonnet, 1957: 2873. Chickering, 1961: 445 [in part only; misidentification, not *M. patruelis* (C. L. Koch)].

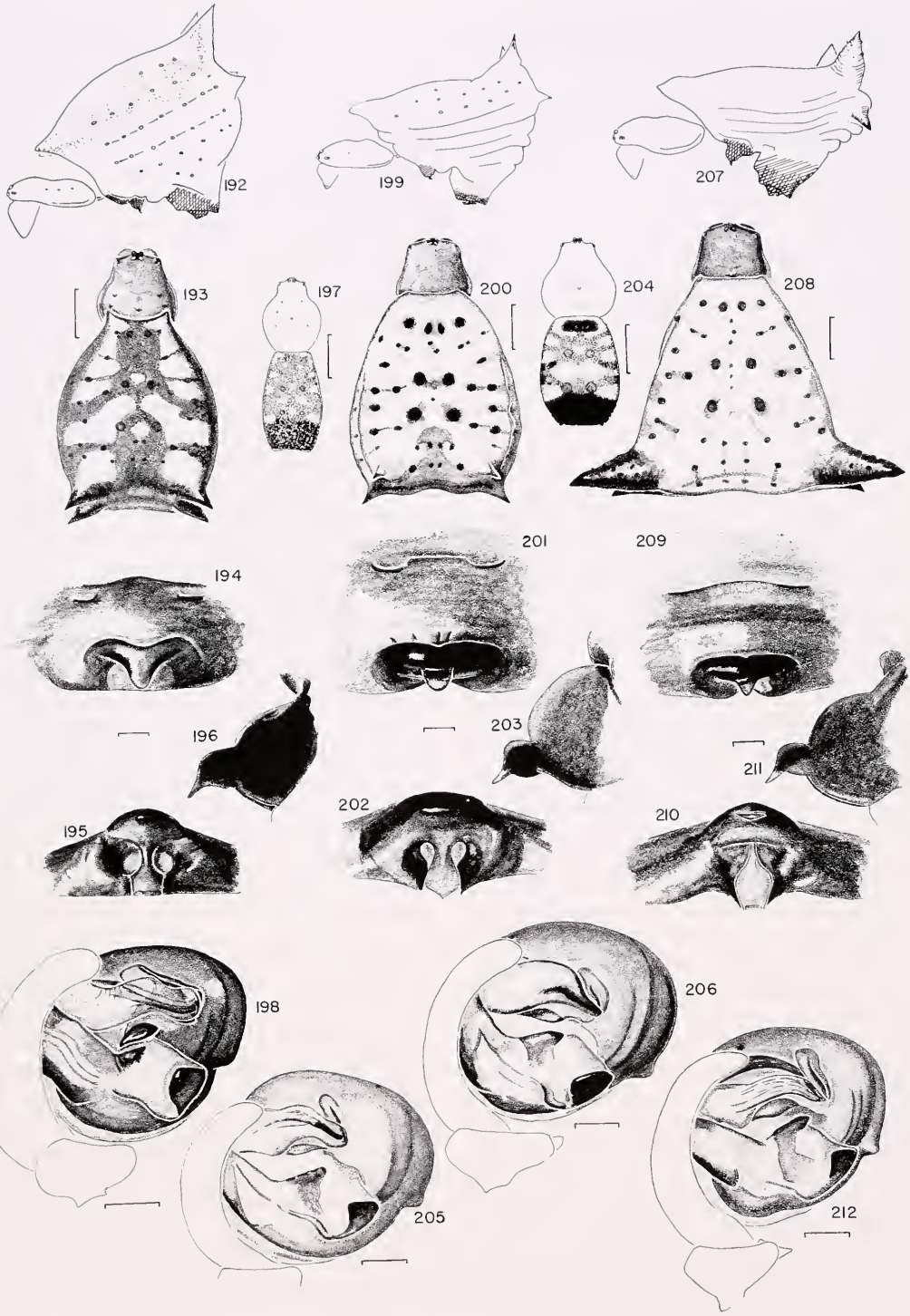
→

Figures 192–198. *Micrathena mitrata* (Hentz). 192–196. Female. 192. Lateral. 193. Dorsal. 194. Epigynum, ventral. 195. Epigynum, posterior. 196. Epigynum, lateral. 197, 198. Male. 197. Dorsal. 198. Left palpus, mesal.

Figures 199–206. *Micrathena patruelis* (C. L. Koch). 199–203. Female. 199. Lateral. 200. Dorsal. 201. Epigynum, ventral. 202. Epigynum, posterior. 203. Epigynum, lateral. 204–206. Male. 204. Dorsal. 205, 206. Palpus, mesal. 205. (Est. Bahia, Brazil). 206. (Prov. Misiones, Argentina).

Figures 207–212. *Micrathena saccata* (C. L. Koch). 207–211. Female. 207. Lateral. 208. Dorsal. 209. Epigynum, ventral. 210. Epigynum, posterior. 211. Epigynum, lateral. 212. Male palpus, mesal.

Scale lines. 0.1 mm, except Figures 192, 193, 197, 199, 200, 204, 207, 208, 1.0 mm.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Micrathena patruelis luteomaculata Strand, 1908: 4. Female holotype from "Popayan oder Cauca" [Popayan, Dept. Cauca], Colombia (SMF), examined. NEW SYNONYMY.

Micrathena patruelis mediovittata Strand, 1908: 4. Two female syntypes from "Popayan oder Cauca" [Popayan, Dept. Cauca], Colombia (SMF), examined. NEW SYNONYMY.

Micrathena mitrata:—Levi, 1978: 428, figs. 28–40, ♀, ♂.

Synonymy. A male from Peru is needed to ascertain the synonymy of *M. peruana*. The holotype of *M. patruelis luteomaculata* has a black and white abdomen; that of *M. patruelis mediovittata* has an orange, leathery abdomen.

In collections most specimens from Mexico and Central America had been misidentified as *M. patruelis*.

Variation. Females from Mexico and Central America vary in total length from 4.1 to 5.6 mm, males from 3.5 to 3.9 mm. Some females are dark colored (Fig. 193), others have only little black pigment on the dorsum; some have anterior humps (Fig. 193), some not. One female from Jalisco, Est. Nayarit, had an additional pair of small lateral humps anterior of the upper posterior spines and had the posterior depressions of the epigynum, with the septum indistinct and the depressions wider. Central American specimens lack the last two pairs of dimples on the carapace; the carapace thus resembles that of *M. saccata*.

Micrathena saccata, M. patruelis and *M. mitrata* are problematic. *Micrathena mitrata* is the common species in eastern North America. *M. saccata* and *patruelis* were described and pictured by C. L. Koch from Brazil (1836: 59 and 1839: 130) illustrating similar abdomens. F. P.-Cambridge (1904: 528) considered specimens from Central America and Mexico to belong to *patruelis* and to differ from *mitrata* by having the upper spines larger than the lower. Reimoser (1917: 80) thought that the lower spines were farther apart than the upper in Mexican and Central American *M. patruelis*, the upper farther apart in *M. mitrata*. He considered *M. saccata* to be the species from Cayenne, Guyana and Venezuela, with longer upper spines than lower (Figs. 207, 208). Chickering (1961) was puzzled by his specimens and illustrated specimens from the Canal Zone as *patruelis*, which Reimoser (and I) have considered *M. saccata*.

In the AMNH collection all specimens from Mexico to Panama had been labeled *patruelis*, and similar specimens from Texas *mitrata*. At first I thought them to be the same, but found that the males from Panama labeled *M. patruelis* (Fig. 212) were distinct from Mexico and Texas males (Fig. 198). Also, *M. mitrata* in the north has six dimples on the thorax (Fig. 188); specimens labeled *M. patruelis* in Central America have only two (Fig. 189). When examining collections from southern Brazil and Argentina I came across other specimens similar to *M. mitrata* (Figs. 199–206), but with the epigynum similar to Panamanian specimens, and a male palpus (Figs. 205, 206) closer to *M. mitrata* from Texas and Mexico. Reexamination of all Mexican and Central American specimens showed two populations in Central America: a smaller, rarer *M. mitrata* (abdomen and epigynum; Figs. 192–195), and a common, larger species with longer upper spines (Figs. 207–210). Here I follow Reimoser, the first reviser, and consider the larger species *M. saccata* and the smaller species *M. mitrata*. I consider the southern South American specimens to belong to a third species, *M. patruelis*. Only the collection of males in intermediate areas will show whether this is correct.

Diagnosis. Females of *M. mitrata* differ from the similar *M. saccata* by having upper and lower spines subequal in size (Figs. 192, 193); in *M. saccata* the dorsal spines are noticeably longer (Figs. 207, 208). The transverse bar of the epigynum is shorter than that of *M. saccata* (Fig. 194), forming with the lobe an almost equilateral triangle (Fig. 194). The largest Central American *M. mitrata* females were 5.6 mm in total length, the smallest

M. saccata 6.0 mm. Females of *M. mitrata* from Mexico and Central America may have slight anterior abdominal humps (Fig. 193).

Males differ from *M. saccata* by having the embolus hidden in mesal view underneath the undulating terminal apophysis (Fig. 198); in *M. saccata* the embolus is arched above the terminal apophysis. The palpus differs from that of *M. bimucronata* by having the conductor (which surrounds the tip of the embolus and terminal apophysis) close to the tip of the cymbium (Fig. 198), while in *M. bimucronata* it is separated from the tip of the cymbium by a distance equal to its own length.

Distribution. Eastern United States to northern South America; absent from the West Indies. Specimen from Acre, Brazil, 6.1 mm in total length, may not be this species. The southernmost males in collections are from Costa Rica (Map 4).

Records. MEXICO: *Est. Tamaulipas.* 65 km S of Linares. *Nuevo Léon.* San Roque; Juárez. *Coahuila.* Simojovel, San Isidro. *San Luis Potosí.* Tamazunchale; 5 km W El Naranjo; Picolo; Huichichuyan; E of Ciudad del Maíz; Valles. *Sinaloa.* Copala; W San Ignacio, 260 m. *Nayarit.* Tepic. *Jalisco.* Plan de Barrancas. *Veracruz.* Fortín de las Flores; El Fortín; Papantla, Cordoba; Chocomán, Tlapacoyan; La Buena Ventura; Atoyac; Mirador Zacuapam, Medias Aguas. *Guerrero.* Acamixtla. *Oaxaca.* Soyaltepec; Tolosa. *Tabasco.* Teapa. *Yucatan.* Colonia Yucatan; Chichen Itza. *Quintana Roo.* Kohunlich ruins, 9 km S Francisco villa. *Chiapas.* Arriago; Montebello; 105 km SE of Palenque; Escuintla; nr. Huehuetan; Huixtla; Palenque ruins; Prusia; Tonalá; Tapachula; Ixtacomitán. GUATEMALA: Variedades; Yepocapa; Guatemala City; Tucuru; Reunion; Ayutla; Coban; Chicacao El Naranjo. HONDURAS: Lancetilla; Tela; Copán. BELIZE: El Cayo. EL SALVADOR: Quetzeltepeque; Santa Tecla; San Salvador. NICARAGUA: San Marcos; Granada. COSTA RICA: *Prov. Puntarenas.* Oza Peninsula, 40 km SW Rincon; Corcovado Natl. Park, Sirena Station; Golfito; Turrialba; San Isidro del General, 650–1,300 m. PANAMA: *Prov. Panamá.* Cerro Galero, 7 Jan. 1977, ♀ (H. Levi, Y. Lubin, MCZ); Summit, July 1950, ♀ (A. M. Chickering, MCZ); Balboa, 3 Aug. 1943, ♀ (J. B. Duncan, AMNH). ECUADOR: *Los Rios Prov.* San Carlos, 1 May 1984, ♀ (F. Manging, MECN). *Pichincha.* km 113 vía Pto. Quito, 19 May 1984, ♀ (L. Avilés, MECN). *Guayas.* Milagro; Colonche A., 1941, ♀ (R. W. Landes, EPC). PERU: *Dept. Junín.* Utcuyacu, March 1948, ♀ (F. Woytkowski, AMNH). BRAZIL: *Est. Acre.* Rio Purus, W of Sena Madureira, 9 Oct. 1973, ♀ (B. Patterson, MCZ).

Micrathena patruelis (C. L. Koch) Figures 199–206; Map 4

Acrosoma patruele C. L. Koch, 1839: 130, pl. 130, fig. 524, ♀. Female from Brazil (ZSM), destroyed.

Note. F. P.-Cambridge, 1904, Reimoser, 1917 and Chickering used the name *patruelis* for southernmost specimens of *Micrathena mitrata. Micrathena mitrata*, however, probably does not occur in Brazil, the type locality. The name has to be used for a very similar species common in southern Brazil.

Description. Female. Carapace, legs dark brown. Sternum blackish brown. Dorsum of abdomen white with black marks (Fig. 200); venter black, sclerotized areas brown. Carapace swollen with a distinct thoracic depression and at most one pair of dimples. Abdomen with four subequal posterior spines (Figs. 199, 200). Total length, 5.4 mm. Carapace, 1.8 mm long, 1.7 mm wide. First femur, 1.6 mm; patella and tibia, 1.7 mm; metatarsus, 1.1 mm; tarsus, 0.6 mm. Second patella and tibia, 1.5 mm; third, 0.9 mm. Fourth femur, 2.0 mm; patella and tibia, 1.6 mm; metatarsus, 1.1 mm; tarsus, 0.6 mm.

Male. Carapace orange. Sternum black. Legs orange. Dorsum of abdomen white and black; venter black with white on each side behind spinnerets. First coxa with

hook. Total length, 4.1 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 1.2 mm; patella and tibia, 1.2 mm; metatarsus, 0.7 mm; tarsus, 0.5 mm. Second patella and tibia, 1.0 mm; third, 0.6 mm. Fourth femur, 1.3 mm; patella and tibia, 1.0 mm; metatarsus, 0.8 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 4.9 to 6.2 mm, males from 3.6 to 4.7 mm. The terminal apophysis of the palpi of the two males examined differs, as does the relative size of the tegulum (Figs. 205, 206) (see discussion under *M. mitrata*).

Diagnosis. Females are difficult to separate from *M. mitrata* found in the northern hemisphere. They differ mainly by having a longer transverse bar in the epigynum and a smaller lobe (Fig. 201). The epigynum thus resembles that of *M. saccata*. Females can be separated from *M. saccata* by having the two pairs of abdominal spines the same size (Figs. 199, 200).

Males have a smaller conductor (Figs. 205, 206) than *M. mitrata*; the terminal apophysis is of different but varying shape (Figs. 205, 206), and the embolus as seen through the terminal apophysis is heavier than that of *mitrata*. The edge of the tegulum is farther away from the conductor than in related species (Figs. 205, 206).

Distribution. Bahia state to northern Argentina. It is uncertain whether some females from Pará belong to this species or to *mitrata*, since we do not have males (Map 4).

Records. BRAZIL: *Est. Bahia.* Iguassú, 1924, 19♀, 3♂ (NRS). *Rio de Janeiro.* Pinheiro, ♀ (MNRJ). *Mato Grosso.* Chavantina, Oct. 1946, ♀ (H. Sick, MZSP). *Mato Grosso do Sul.* Três Lagoas, 20 May 1964, ♀ (MZSP). *São Paulo.* Ourinhos, 1901, ♀ (T. Lima, MZSP). PARAGUAY: *Dept. Amamtay.* P. N. Cerro Caré, May–June 1982, ♀ (J. A. Kochalka, JAK). *Concepción.* Territ. Foncière, 1908, 2♀ (E. Reimoser, NMW). ARGENTINA: *Misiones Prov.* Montecarlo, 3 Dec. 1965, ♀ (Giaschi, AMNH); Pto. 17 de Octobre, Oct. 1953, 20♀, 3♂ (De Carlo *et al.*, MACN); San Ignacio, Dec. 1948, 4♀ (M. Birabén, MULP). *Salta.* ?Tabacal, ♀ (33484, MACN).

Micrathena saccata (C. L. Koch)
Plate 2; Figures 189–191, 207–217; Map 4

Acrosoma saccatum C. L. Koch, 1836: 59, pl. 59, fig. 212, ♀. Female specimen from Brazil (ZSM), destroyed.

? *Micrathena imbellis* Simon, 1895: 854, fig. 916; 1896: 49. Three juvenile syntypes from Corosal [10 km W of Caracas] and San Esteban [6 km S of Puerto Cabello], Venezuela (No. 10009, MNHN), examined. NEW SYNONYMY.

Micrathena patruelis:—F. P.-Cambridge, 1904: 533, pl. 50, figs. 15, 16, ♀, ♂ (in part). Reimoser, 1917: 102, pl. 4, fig. 7, ♀ (in part). Roewer, 1942: 960. Bonnet, 1957: 2873. Chickering, 1961: 445, figs. 138–145, ♀, ♂. [in part only, misidentification; not *M. patruelis* (C. L. Koch)].

Micrathena saccata:—Reimoser, 1917: 123, pl. 8, fig. 22, ♀. Roewer, 1942: 962. Bonnet, 1957: 2876.

Micrathena retracta Chamberlin and Ivie, 1936: 57, fig. 131, ♀. Female holotype from Barro Colorado Island, Panama (AMNH), examined. First synonymized with *patruelis* by Chickering. NEW SYNONYMY.

Micrathena timida di Caporiacco, 1947: 21. Juvenile holotype from British Guyana (MZUF), examined; 1948: 667, fig. 79. NEW SYNONYMY.

Synonymy. The largest specimen of *M. imbellis* is a juvenile lacking posterior spines on the abdomen, as do immature males. Another specimen is an immature male; the smallest is 2.0 mm long without spines. The specimens are illustrated (Figs. 190, 191); they may be *M. mitrata*. *Micrathena timida* is an immature.

Description. Female. Carapace, sternum dark brown. Legs and coxae dark brown. Dorsum of abdomen white with some black marks (Fig. 208); venter black with some white patches behind. Carapace swollen with distinct thoracic depression and one pair of indistinct dimples, or dimples absent (Fig. 189). Abdomen with two pairs of spines, upper pair longest (Figs. 207, 208, 213, 214). Total length, 6.5 mm. Carapace, 2.4 mm long, 2.0 mm wide. First femur, 2.0 mm; patella and tibia, 2.0 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm. Second patella and tibia, 1.9 mm; third, 1.2 mm. Fourth fe-

mur, 2.4 mm; patella and tibia, 1.9 mm; metatarsus, 1.4 mm; tarsus, 0.6 mm.

Male. Carapace, legs brown. Sternum dark. Dorsum of abdomen with black pigment and white pigment in paired white patches surrounded by zone free of black. Thorax with median mark. Small hook on first coxa and groove on second femur. Abdomen relatively short, rectangular. Total length, 3.7 mm. Carapace, 1.7 mm long, 1.4 mm wide. First femur, 1.4 mm; patella and tibia, 1.4 mm; metatarsus, 1.0 mm; tarsus, 0.6 mm. Second patella and tibia, 1.2 mm; third, 0.7 mm. Fourth femur, 1.6 mm; patella and tibia, 1.3 mm; metatarsus, 0.9 mm; tarsus, 0.6 mm.

Variation. Females vary in total length from 6.0 to 6.8 mm in Central America; the smallest came from Guyana and Brazil and were 5.5 mm. Males vary in total length from 3.2 to 3.7 mm. The carapace of females lacks dimples; sometimes only the first pair is present, the other indistinct. The abdomen of females is very variable. Specimens from Guyana had the longest upper spines. This species appears distinct from the sympatric *M. mitrata*, but is it distinct from *M. patruelis*? (see discussion under *M. mitrata*). One specimen from Trinidad has a leathery abdomen and was first considered distinct (Figs. 213–217).

Note. Chickering first matched males with females.

Diagnosis. Micrathena saccata is always larger than sympatric specimens of *M. mitrata* in Central America. The epigynum has a longer transverse bar than that of *M. mitrata* and the lobe is relatively smaller (Figs. 209, 215). The upper spines are always longer than the lower (Figs. 207, 208, 213, 214). Males are separated by the curved terminal apophysis and embolus arched above this structure, permitting the embolus to be visible (Fig. 212).

Distribution. Honduras to central South America (Map 4).

Records. HONDURAS: *Dept. Atlántida.* Tela, ♀ (A. M. Chickering, MCZ). COSTA RICA: *Cartago Prov.* Turrialba, 15 Aug. 1963, ♂ (W. Peck, EPC). PANAMA: *Prov. Panamá.* El Valle; Fort Davis; Barro Colorado Island; Gamboa; Madden Dam area; Summit; Fort Randolph; Taboga Island. TRINIDAD: Navy base, SW Trinidad, ♀. VENEZUELA: *Est. Carabobo.* San Esteban, Jan. 1940, 3 imm., 3♀ (P. Andruze, AMNH). *Dist. Fed.* Caracas, 4♀ (NMW). GUYANA: *Essequibo Distr.* Onoro region, upper Essequibo Riv., Dec. 1937, ♀ (W. G. Hassler, AMNH). *Bartica.* Kartabo, many coll. (CUC, AMNH). FRENCH GUIANA: Cayenne, ♀ (K. Jelski, PAN). Port du Salut, ♀ (K. Jelski, PAN). COLOMBIA: *Dept. Magdalena.* Río Frío, 8 Aug. 1926, ♀ (F. W. Walker, AMNH). *Meta.* 45 km W of Villavicencio, 1,500 m, June 1947, ♀ (L. Richter, AMNH). ECUADOR: *Prov. Los Rios.* Pichilingue, 2 Feb. 1955, ♀ (E. I. Schlinger, E. S. Ross, CAS). *Guayas.* Zápotal, 7 April 1941, ♀, ♂ (J. Barrett, EPC). PERU: *Dept. Huánuco.* 110 km E of Tingo María, 11 Dec. 1954, imm. (E. I. Schlinger, E. S. Ross, CAS). *Loreto.* Río Samiria, Oct. 1912, ♀ (Bluntschli-Beyer, AMNH). BRAZIL: *Est. Pará.* Belém, July 1972, 3♀ (D. G. McGrath, MCZ; M. Galiano, MEG); 50 km E of Canindé, Rio Gurupi, 1963, ♀ (B. Malkin, AMNH, MZSP); Canindé, Oct. 1964, ♀ (B. Malkin, AMNH); Jacazeacanga, Oct. 1959, ♀ (M. Alvarenga, AMNH). *Mato Grosso.* Barra do Tapirapé, 15–25 July 1963, ♀ (B. Malkin, AMNH). *Rondônia.* Abunã, March 1922, ♀ (J. H. Williamson, MCZ).

Micrathena cubana (Banks)
Figures 218–224; Map 4

Acrosoma cubana Banks, 1909a: 163, pl. 45, fig. 2. Juvenile holotype from San Diego de Los Baños [Pinar del Río Prov.], Cuba (MCZ), lost.

Micrathena reduviana var. *alba* Franganillo, 1936: 47, fig. 50, ♀. NEW SYNONYMY.

Micrathena reduviana var. *rufa* Franganillo, 1936: 98. NEW SYNONYMY.

Micrathena cubana:—Bryant, 1940: 371, figs. 137, 138, 144, 152, 153, ♀ (not male). Roewer, 1942: 956. Bonnet, 1957: 2865. Chickering, 1964: 256, figs. 4–7, ♀.

Micrathena forcipata:—Bryant, 1940: 372, figs. 141,

146, ♂. Chickering, 1964: 257, fig. 16, ♂. (Male only; misidentification, not *M. forcipata*).

Description. Female. Carapace, sternum, legs dark brown. Dorsum of abdomen with black T-shaped patch on white (Fig. 219); sides black with some white spots; venter black. Carapace with three pairs of dimples, a circular thoracic depression, and a narrow, light rim. Femora corniculate. Abdomen with pair of short, soft anterior tubercles, one pair large posterior upper spines, a smaller pair below (Figs. 218, 219); upper spines with some tubercles bearing setae. Total length, 7.0 mm. Carapace, 2.4 mm long, 2.1 mm wide. First femur, 2.2 mm; patella and tibia, 2.3 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm. Second patella and tibia, 2.0 mm; third, 1.2 mm. Fourth femur, 2.7 mm; patella and tibia, 2.2 mm; metatarsus, 1.6 mm; tarsus, 0.6 mm.

Male. Carapace, sternum, legs brown. Dorsum of abdomen with white patches on brown background (Fig. 223); venter black. Carapace with two or three pairs of dimples and a thoracic depression. Hook on first coxa. Sides of abdomen parallel, posterior rounded (Fig. 223). Total length, 3.6 mm. Carapace, 1.0 mm long, 0.6 mm wide. First femur, 1.4 mm; patella and tibia, 1.5 mm; metatarsus, 1.2 mm; tarsus, 0.5 mm. Second patella and tibia, 1.3 mm; third, 0.7 mm. Fourth femur, 1.7 mm; patella and tibia, 1.2 mm; metatarsus, 1.0 mm.

Variation. Females vary in total length from 4.8 to 6.8 mm, males 3.5 to 3.6 mm. All females and juveniles examined had similar black marks on the dorsum of the abdomen. Another male had the conductor and the paramedian apophysis relatively larger than the one illustrated (Fig. 224), but of the same shape.

Note. Even though the male had been collected with females and has the palpus like that of the related *M. mitrata* and *M. saccata*, Bryant and Chickering mistook the male to be that of *M. forcipata*.

Diagnosis. The black T-shaped patch on the dorsum of the abdomen and the shape of the abdomen (Figs. 218, 219) distinguish females from *M. mitrata* and *M. saccata*, neither of which occurs in Cuba. Males differ from these two similar species by the shape of the conductor, which has a slit (Fig. 224). The embolus when viewed through the terminal apophysis has a biforked tip (Fig. 224).

Natural History. Micrathena cubana has been collected from gardens, woods and a ravine in mountain forest at an elevation of 600 to 1,000 m.

Distribution. Cuba (Map 4).

Records. CUBA: *Santiago Prov.* Sierra del Cobra, Loma del Gato, 800–1,000 m, 7♀, ♂ (MCZ), 5♀ (AMNH); Jiguaní, Los Negros, ♀ (MCZ); Jiguaní, Los Altos, ♀ (MCZ); coast below Pico Turquino, ♀ (MCZ); Puerto Boniato, ♀ (AMNH), ♀ (L. F. Armas, CASH); Río Piloto, Sierra de Nipe, ♀ (R. Bielanski, A. Riedel, PAN). *Guantánamo.* N of Imías, 900–1,200 m, 2♀ (MCZ); Cuchillo de Guájimero, 600 m, ♀ (MCZ); Gran Piedra, ♀ (AMNH); Monte Verde, ♀ (O. Garrido, J. de la Cruz, CASH). *Cienfuegos.* Soledad, ♀ (MCZ); Trinidad, Mina Carlotta, ♀ (many coll., MCZ); Sierra Trinidad, Buenos Aires, 750–1,050 m, ♀, ♂ (MCZ); Trinidad Mts., 750 m, ♀ (MCZ), 7

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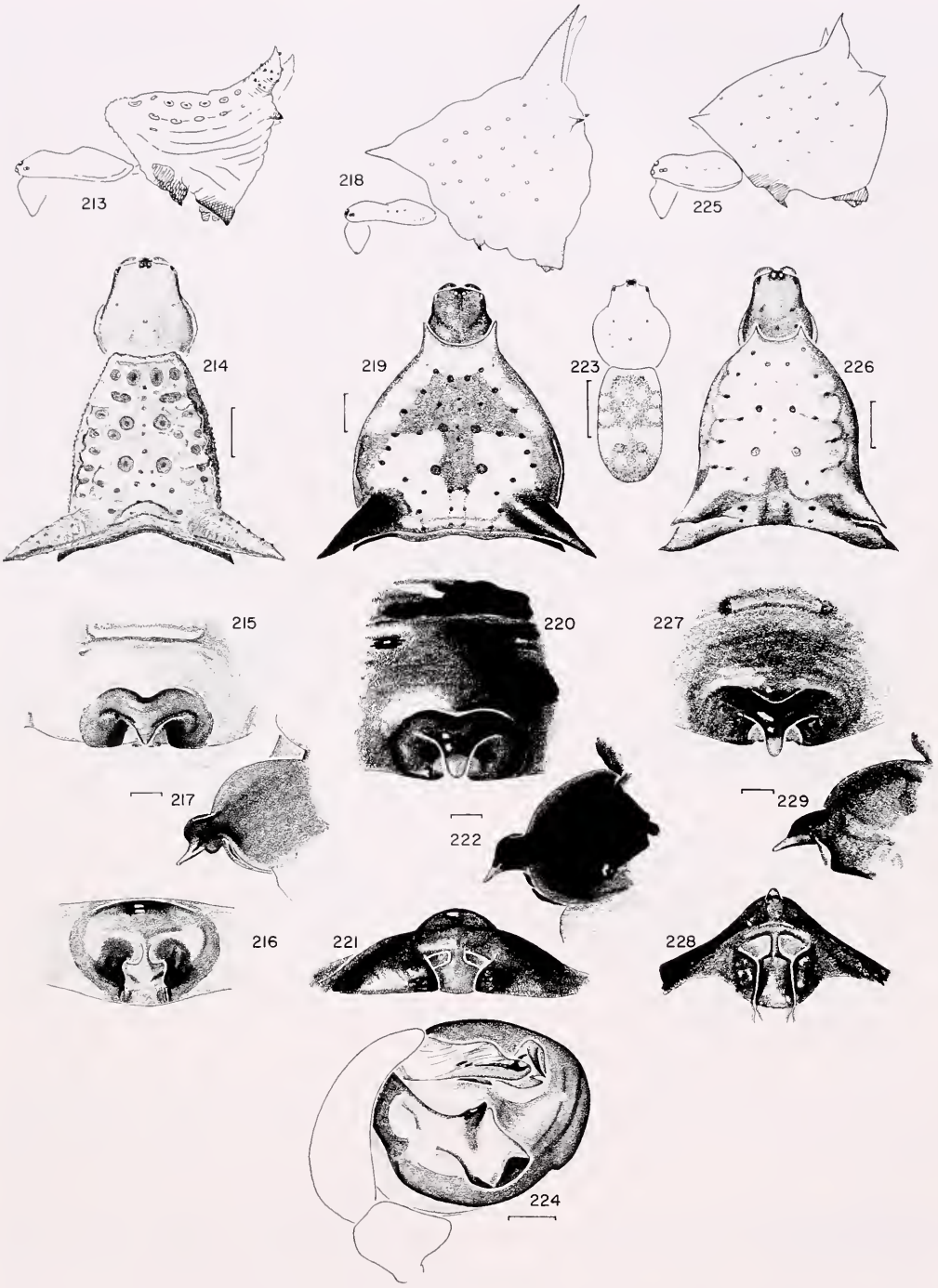
Figures 213–217. *Micrathena saccata* (C. L. Koch) (Trinidad), female. 213. Lateral. 214. Dorsal. 215. Epigynum, ventral. 216. Epigynum, posterior. 217. Epigynum, lateral.

Figures 218–224. *Micrathena cubana* Bryant. 218–222. Female. 218. Lateral. 219. Dorsal. 220. Epigynum, ventral. 221. Epigynum, posterior. 222. Epigynum, lateral. 223, 224. Male. 223. Dorsal. 224. Left palpus, mesal.

Figures 225–229. *Micrathena similis* Bryant, female. 225. Lateral. 226. Dorsal. 227. Epigynum, ventral. 228. Epigynum, posterior. 229. Epigynum, lateral.

Scale lines. 0.1 mm, except Figures 213, 214, 218, 219, 223, 225, 226, 1.0 mm.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Sept. 1972, ♀ (L. F. Armas, CASH); San Blas, ♀ (MCZ). *Pinar del Río.* San Vicente, ♀ (AMNH); Viñales, ♀ (AMNH); Candelaria, 2♀ (MCZ). *Villa Clara.* Vega Alta, ♀ (CUC); Topes de Collantes, ♀ (AMNH).

Micrathena similis Bryant
Figures 225–229; Map 4

Micrathena similis Bryant, 1945: 45, figs. 8, 43, 44, ♀. Female holotype from Puerto Plata, Dominican Republic (MCZ), examined. Chickering, 1964: 279, figs. 68–71, ♀.

Description. Female holotype. Carapace brown with light brown rim. Sternum, legs brown. Dorsum of abdomen white, sides and venter black. Carapace with three pairs of dimples (Figs. 225, 226). Total length, 5.5 mm. Carapace, 2.2 mm long, 1.8 mm wide. First femur, 1.8 mm; patella and tibia. 1.9 mm; metatarsus, 1.4 mm; tarsus, 0.4 mm. Second patella and tibia, 1.8 mm; third, 1.1 mm. Fourth femur, 2.3 mm; patella and tibia, 1.7 mm; metatarsus, 1.3 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 5.1 to 5.5 mm. The holotype has the dorsum of the abdomen white; that of the paratype is black like that of some *M. mitrata.*

Note. The male is unknown.

Diagnosis. The female differs from most Florida *M. mitrata* by having an anterior pair of humps overhanging the carapace (Fig. 226). It differs from *M. cubana* by the differently shaped abdomen and the different markings (Fig. 226).

Distribution. Hispaniola (Map 4).

Records. DOMINICAN REPUBLIC: *Prov. Puerto Plata.* Mt. Diego de Ocampo, North Range, 900–1,200 m, July 1938, ♀ (P. J. Darlington, MCZ). *Barahona.* Valle de Polo, 700–850 m, 18 Aug. 1935, ♀ (W. G. Hassler, AMNH).

Micrathena coroico new species
Figures 230–234; Map 5

Holotype. Female from Coroico, Dept. La Paz, Bolivia (NMW). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace light orange with median and two lateral darker streaks. Labium, endites, sternum blackish brown. Coxae very light, distal leg articles light orange. Dorsum of abdomen whitish with dark sclerotized spots and tips of spines black (Fig. 231); venter with book-lung covers dark brown, otherwise mottled black and white. Carapace with three pairs of indistinct dimples indicated by darker streaks; thorax high (Fig. 231), with distinct thoracic depression. Posterior median eyes 1.2 diameters of anterior medians; laterals slightly smaller than anterior median eyes. Abdomen with one pair of spines overhanging carapace and two posterior pairs (Fig. 231). Total length, 10.4 mm. Carapace, 3.7 mm long, 3.0 mm wide. First femur, 4.1 mm; patella and tibia, 4.2 mm; metatarsus, 2.9 mm; tarsus, 1.2 mm. Second patella and tibia, 3.8 mm; third, 2.0 mm. Fourth femur, 5.0 mm; patella and tibia, 4.2 mm; metatarsus, 3.2 mm; tarsus, 1.2 mm.

Diagnosis. Micrathena coroico differs from *M. macfarlanei* and other similar species by having no lateral spines (Figs. 230, 231).

Micrathena crassispina (C. L. Koch)
Figures 235–241; Map 5

Acrosoma crassispinum C. L. Koch, 1836: 55, fig. 209, ♀. Female from America, lost.

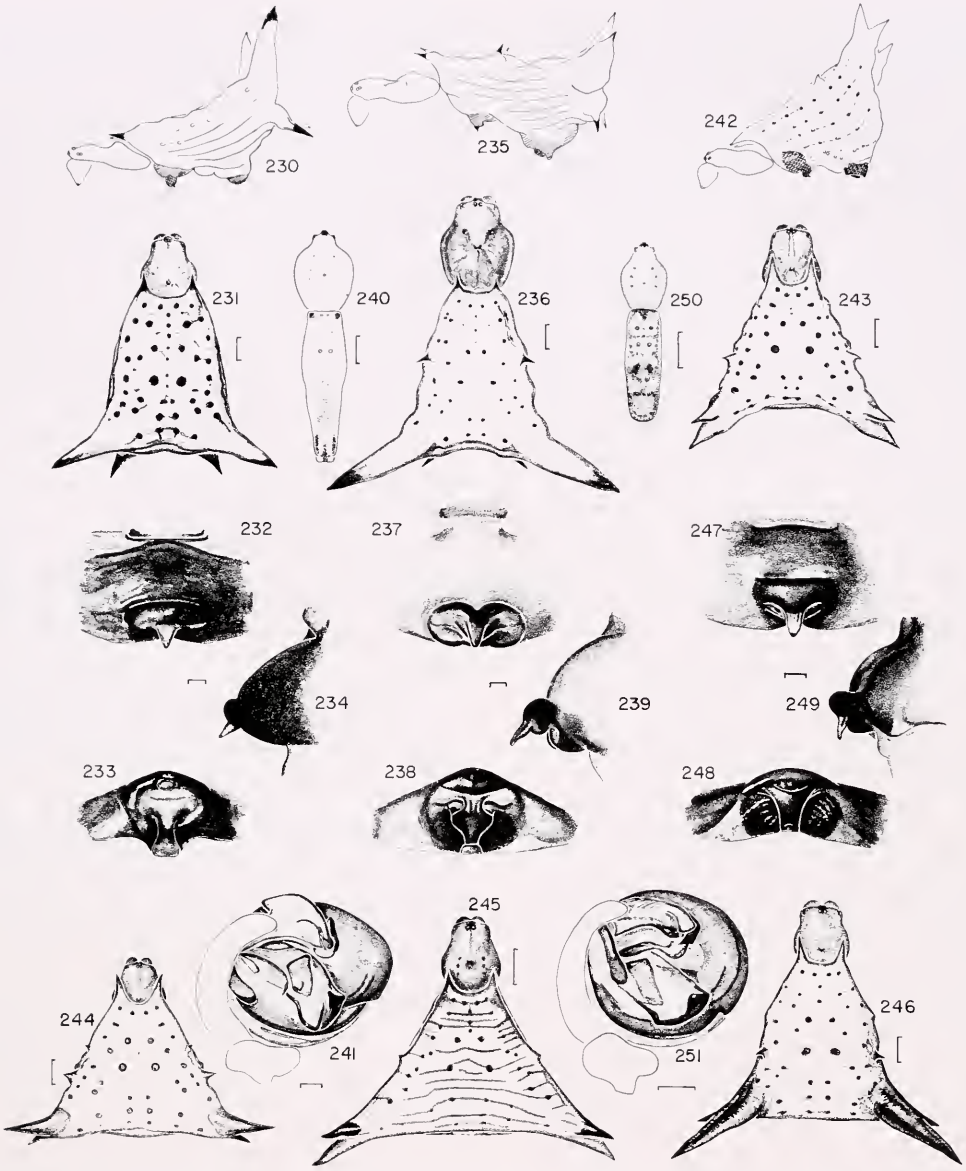
Micrathena bergi Simon, 1901: 121. Female from Chaco, Argentina (MNHN), lost. NEW SYNONYMY.

Micrathena spinosa:—Mello-Leitão, 1939: 72, figs. 54, 55, ♀ (misidentification).

Micrathena crassispina:—Roewer, 1942: 956. Bonnet, 1957: 2864.

Synonymy. This species best fits Koch's original description and the illustration of a pinned specimen. Simon's description of *M. bergi*, the type of which is lost, also fits this species.

Description. Female. Carapace, sternum, legs orange. Abdomen white with tips of spines black. Carapace with a deep dimple on each side behind head; thorax high; rim indistinct but present. Abdomen subtriangular with four pairs of spines



Figures 230–234. *Micrathena coroico* n. sp., female. 230. Lateral. 231. Dorsal. 232. Epigynum, ventral. 233. Epigynum, posterior. 234. Epigynum, lateral.

Figures 235–241. *Micrathena crassispina* (C. L. Koch). 235–239. Female. 235. Lateral. 236. Dorsal. 237. Epigynum, ventral. 238. Epigynum, posterior. 239. Epigynum, lateral. 240, 241. Male. 240. Dorsum. 241. Left palpus, mesal.

Figures 242–251. *Micrathena lucasi* (Keyserling). 242–249. Female. 242. Lateral. 243–246. Dorsal. 243. (Lectotype, Bogotá). 244. (Lectotype, *M. acutospina,* Bogotá). 245. (Dept. Junín, Peru). 246. (Boquete, Panamá). 247. Epigynum, ventral. 248. Epigynum, posterior. 249. Epigynum, lateral. 250, 251. Male. 250. Dorsal. 251. Palpus, mesal.

Scale lines. 0.1 mm, except Figures 230, 231, 235, 236, 240, 242–246, 250, 1.0 mm.

(Figs. 235, 236). Total length, 11.5 mm. Carapace, 4.3 mm long, 3.5 mm wide. First femur, 4.8 mm; patella and tibia, 4.7 mm; metatarsus, 3.4 mm; tarsus, 1.4 mm. Second patella and tibia, 4.2 mm; third, 2.6 mm. Fourth femur, 5.8 mm; patella and tibia, 4.7 mm; metatarsus, 3.4 mm; tarsus, 1.3 mm.

Male. Carapace orange, sides brown. Sternum light orange, legs orange. Dorsum of abdomen with anterolateral black patches and posterior dark marks; venter with book-lungs dark, no pigment in midline; black on sides; black around spinnerets and posterior to spinnerets. Carapace with three pairs of indistinct dimples and very distinct thoracic depression. Length of abdomen more than 3.5 times anterior width, narrowing behind (Fig. 240). First coxa with hook, second femur with groove. Total length, 8.2 mm. Carapace, 3.0 mm long, 2.3 mm wide. First femur, 2.9 mm; patella and tibia, 2.2 mm; metatarsus, 2.2 mm; tarsus, 0.9 mm. Second patella and tibia, 2.2 mm; third, 1.2 mm. Fourth femur, 3.3 mm; patella and tibia, 2.4 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm.

Variation. Females vary in total length from 9.4 to 11.5 mm, males from 7.7 to 8.6 mm. Females sometimes have a minute spine pair below the posterior pair of spines.

Note. Males have been collected with immature and adult females.

Diagnosis. Micrathena crassispina differs from *M. guanabara* by having one less pair of spines on the posterior of the abdomen, from *M. raimondi* and *M. miles* by having a pair of spines overhanging the carapace (Figs. 235, 236), and from all three by the shape of the posterior face of the epigynum (Figs. 237–239).

Distribution. Southern Brazil, Bolivia to northern Argentina (Map 5).

Records. BRAZIL: *Est. Espírito Santo.* Rio São José, ♀ (MZSP). *Rio de Janeiro.* Niterói, 2♀ (MNRJ). *São Paulo.* São Paulo, 4♀ (MNRJ, BMNH, MZSP); Boracéia, ♀ (MZSP). *Paraná.* Curitiba, ♀ (MZSP); Banhado, ♀ (MZSP). *Santa Catarina.* Serra Geral, ♀ (ZMB); Nova Teutonia, ♀ (CAS); Lagoa, ♀ (IBSP); Blumenau, ♀ (NMW). *Rio Grande do Sul.* Guarani, ♀ (AMNH); Pelotas, ♀ (AMNH); Triunfo, 4♀, 3♂ (FZRS); Montenegro, 3♂ (FZRS); Viamao, 4♀ (FZRS); São Franciso de Paula, ♀ (FZRS); Garruchos, São Borja, ♂ (FZRS); Passo Fundo, 6♀ (IBSP). BOLIVIA: *Dept. Potosí.* Cornaca, ♀ (MCZ). PARAGUAY: 2♀ (NHMB, BMNH). ARGENTINA: *Prov. Misiones.* Puerto Aguirre, ♀ (MULP); Pindpoy, ♀ (MULP); San Ignacio, ♀ (MULP); Santa Maria, ♀ (MACN), 8♀, 3♂ (MACN); Santa Ana, 2♀ (MACN); Punto Tabay, 4♀ (MACN); Eldorado, ♀ (IMLT); Monteagudo, 26♀, 10 imm. (MACN).

Micrathena lucasi (Keyserling)
Figures 242–251; Map 5

Acrosoma lucasi Keyserling, 1863: 68, pl. 2, fig. 1, ♀. Female lectotype designated by Chickering, 1960c, and nine female, two juvenile paralectotypes from Bogotá, Colombia (BMNH), examined. 1892: 27, pl. 1, fig. 24.

Acrosoma acutospinum Keyserling, 1863: 69, pl. 2, fig. 3, ♀. Female lectotype and four female paralectotypes from Santa Fé de Bogota, N. Granada [Bogotá, Colombia] (BMNH), designated by Chickering, 1960c, examined; 1892: 26, pl. 1, fig. 23, ♀. NEW SYNONYMY.

Acrosoma occidentalis Taczanowski, 1879: 111, pl. 1, fig. 28, ♀. Three female syntypes from Amable María [Junín], Peru (PAN), examined. NEW SYNONYMY.

Acrosoma trapa Gétaz, 1893: 105. Three females from Buenos Aires [Prov. Puntarenas], Costa Rica, lost. NEW SYNONYMY.

Micrathena inaequalis F. P.-Cambridge, 1904: 535, pl. 50, fig. 20, ♀. Four female syntypes from Volcán de Fuego [14°29'N, 90°53'W], Guatemala (BMNH), examined. Reimoser, 1917: 116. Roewer 1942: 959. Bonnet, 1957: 2870. Chickering, 1961: 427, figs. 89–93, ♀. NEW SYNONYMY.

Micrathena joinvillicola Strand, 1915: 121. Juvenile holotype from Joinville, Santa Catarina, Brazil (SMF), examined. NEW SYNONYMY.

Micrathena occidentalis:—Reimoser, 1917: 112, pl. 6, fig. 16, ♀. Roewer, 1942: 960. Bonnet, 1957: 2873.

Micrathena acutospina:—Reimoser, 1917: 115. Roewer, 1942: 953. Bonnet, 1957: 2861. Chickering, 1960c: 66, figs. 1–3, ♀.

Micrathena lucasi:—Reimoser, 1917: 117. Roewer, 1942: 959. Bonnet, 1957: 2871. Chickering, 1960c: 82, figs. 63–65.

Synonymy. Keyserling wrote that he had only one specimen of *M. acutospina.* Others may have been added to the vial

at a later time. *Micrathena lucasi* and *M. acutospina* were described by Keyserling at the same time; the syntypes of the two names differ: *M. acutospina* (Fig. 244) has an additional pair of denticles anterior on the sides which *M. lucasi* lacks (Fig. 243). There are also slight differences in proportions and swellings of the posterior view of the epigyna and internal genitalia. Many other specimens from various collections seem to be intermediate, in both the posterior view of the epigynum and the presence or absence of the denticle. Some specimens have a slight hump in its place; others a denticle only on one side. Perhaps the two original collections of Keyserling, both allegedly from Bogotá, came from different localities. In the early 19th century Bogotá was a trading center for natural history specimens, and the specimens may have been bought rather than collected there.

Micrathena occidentalis differs by having a relatively wide abdomen with transverse stripes (Fig. 245). The thorax is high, the dimples more distinct (Figs. 245), and the lobe of the epigynum blunter. There are only a few specimens in collections resembling the types: Villavicencio, Colombia; S of Santo Domingo, Ecuador and some from southern Brazil. One female from Villavicencio had an asymmetrical abdomen, wider on one side than the other. Finding the males that belong with the striped females may indicate whether or not this is a distinct species.

Gétaz' description and measurements of *Acrosoma trapa* fit this species and not others. Gétaz did not notice the tiny spines on the sides of the abdomen.

Micrathena inaequalis types are close to those of *M. lucasi* and without doubt the same species; the type of *M. joinvillicola* is an immature.

Description. Female lectotype of *M. lucasi.* Carapace, legs, sternum brown. Dorsum of abdomen whitish; posterolateral spines with some black pigment; sides and venter with some gray marks. Epigynum and ring around spinnerets brown. Carapace with three pairs of indistinct dimples and a round thoracic depression. Abdomen with eight spines, the posterolaterals subequal in size (Figs. 242, 243). Total length, 6.8 mm. Carapace, 2.7 mm long, 2.2 mm wide. First femur, 2.5 mm; patella and tibia, 2.6 mm; metatarsus, 1.8 mm; tarsus, 0.6 mm. Second patella and tibia, 2.4 mm; third, 1.4 mm. Fourth femur, 2.7 mm; patella and tibia, 2.4 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm.

Male from Dept. Valle, Colombia. Carapace brown, sides darker, grayish. Sternum blackish brown. Legs brown, femora darkest. Dorsum of abdomen with rim of black pigment around margin on yellow-brown background; sclerotized disks black; indications of two white transverse bands; venter black without marks. Carapace with faint dimples (Fig. 250). First coxa with hook, second femur with groove. Abdomen longer than wide, sides parallel, rounded behind (Fig. 250). Total length, 4.8 mm. Carapace, 2.0 mm long, 1.4 mm wide. First femur, 1.5 mm; patella and tibia, 1.4 mm; metatarsus, 1.0 mm; tarsus, 0.6 mm. Second patella and tibia, 1.3 mm; third, 0.8 mm. Fourth femur, 1.7 mm; patella and tibia. 1.3 mm; metatarsus, 0.9 mm; tarsus, 0.6 mm.

Variation. Females of *M. lucasi* are extremely variable, ranging in total length from 5.4 to 8.3 mm. Males vary in total length from 4.5 to 4.8 mm. The thorax of some specimens is higher than in others, and the dimples more distinct (independent of the striped abdomen). Most specimens have the abdomen longer than wide to as long as wide, but there are some that have the abdomen much wider than long (Fig. 245). Some have the socket of the posterolateral spines extended (Fig. 246). One female from San José, Costa Rica had the ventral one of the double spines reduced to a large denticle (perhaps it belonged to a different species).

Note. One collection had a large series of males and females, another a male and a female collected together. Late immature stages have an abdomen like the adult.

Diagnosis. The eight-spined female (sometimes an additional pair of lateral

denticles is present) differs from *M. crassispina*, which also has eight spines, by the first pair overhanging the carapace being usually white, and by the third and fourth pair having a common socket (Figs. 242–246). The T-shaped epigynum usually has a narrow, light colored lobe (Fig. 247). In posterior view there is a swelling in the throat, often lighter colored and continuing dorsally in the middle. It is bordered on each side by a heavier, sclerotized area, sometimes dark colored (Fig. 248).

Males differ from others by the sclerotized plate on the proximal end of the median apophysis, the terminal apophysis having a wide overhanging appendage, and by the sclerotized conductor visible behind the tip of the embolus and terminal apophysis (Fig. 251).

Natural History. Micrathena lucasi is a montane species occurring 1,000 to 2,300 m elevation in Mexico, in the mountains of Panama, and at higher elevations through Colombia to Peru. It is found in forests, with one record from a paramo in the Sierra de Santa Marta.

Distribution. Mexico to southern Brazil (Map 5).

Records. MEXICO: *Est. Veracruz.* Volcán San Martín, nr. San Andrés Tuxtla, 1,000 m, July 1953, ♀ (C. J. Goodnight, AMNH). *Oaxaca.* Yelagago, 2,300 m, 1963, ♀. *Chiapas.* Cacahuatán, 1,200–1,500 m, 2♀ (AMNH); Finca "La Isle," 2♀ (CAS). GUATEMALA: Chicacao, El Naranjo, ♀ (AMNH). COSTA RICA: *Alajuela Prov.* Est. Fabio Baudrit, 2♀ (MZCR). *Cartago.* Finca Sinfonía [9:50N, 83:05W], ♀ (AMNH); nr. Turrialba, 1,300 m, ♀ (MCZ), 3♀ (MZCR); Juan Viñas, ♀ (NMW). *San José.* San José, 1,100 m, ♀ (AMNH, MCZ); Ciudad Universitaria, ♀ (MZCR); Potorro, 1,600 m, 4♀ (MCZR). *Puntarenas.* San Vito, 2♀ (AMNH, MZSR). La Verbena, ♀ (MCZ); Monteverde, 2♀ (AMNH, MCZ). *Cartago.* San Isidro del General, 600–1,200 m (MCZ). PANAMA: *Prov. Chiriquí.* El Volcán, ♀ (AMNH), ♀, ♂ (MCZ); Boquete, ♀ (MCZ); La Fortuna dam site, 2♀ (MCZ). *Panamá.* El Valle, ♀ (MCZ); El Valle de Antón, ♀ (UPMI). VENEZUELA: *Est. Monagas.* Caripito, ♀ (FSCA). *Aragua.* Maracay, ♀ (AMNH). COLOMBIA: *Dept. Magdalena.* Sierra Nevada de Santa Marta: San Pedro de la Sierra, 1,400 m, ♀ (MCZ), San Pedro, 1,100 m, 4♀ (JAK), Serra Nueva Granada, 1,700 m, ♀ (JAK), Donachui, 2♀ (JAK). *Cesar.* Sierra de Perijo, Socorpa Mission, 1,500–1,600 m, 2♀ (AMNH). *Antioquia.* Medellín, ♀ (MCZ); La Estrella, 2,100 m, ♀ (MCZ). *Boyacá.* Río Dpan, 850–950 m, ♀ (AMNH). *Cundinamarca.* Bogotá (MCZ); El Colegio, ♀ (CAS). *Meta.* Villavicencio, 2♀ (AMNH, CAS). *Valle.* Lago Calima, ♀ (MCZ); Cali, ♀ (CAS, MCZ); 90 km S of Cali, 1,700 m, ♀ (MCZ); Pichinda, 1,700 m, ♀, ♂ (MCZ); Yotoco, 2♂ (MCZ). *Cauca.* Piendamó, ♀ (MCZ); Popayán, ♀ (CAS). *Huila.* Inzá, 1,700 m, 2♀ (MCZ). ECUADOR: *Imbabura Prov.* Paramba, 2♀ (BMNH). *Pichincha.* 47 km S of Sto. Domingo, ♀ (MCZ). *Bolívar.* Balzapamba, 5♀ (AMNH), 11♀, 4 imm., 9♂ (AMNH), 700 m, ♂, 2 imm. (AMNH). PERU: *Dept. San Martín.* 20 km SE Moyobamba, June 1947, ♀ (AMNH). *Amazonas.* Santa Rosa, Río Chinchipe, 1,600 m, July 1947, ♀ (EPC). BRAZIL: *Est. Pará.* 3°10′S, 47°30′W, km 305 Rodovia Belém-Brasília, ♀ (MZSP). *Minas Gerais.* Viçosa, 2♀ (IBSP). *São Paulo.* Caraquatatuba, ♀ (MZSP); Ourinhos, ♀ (MZSP). *Santa Catarina.* ♀ (E. Reimoser, MCZ), 3♀ (NMW).

Micrathena macfarlanei Chickering
Figures 252–260; Map 5

Micrathena macfarlanei Chickering, 1961: 430, figs. 99–102, ♀. Female holotype from Barro Colorado Island, Panama (MCZ), examined.

Micrathena melloleitaoi Archer, 1971: 157, fig. 6, ♀. Female holotype from Tingo María, Huánuco, Peru (AMNH), examined. NEW SYNONYMY.

Description. Female from Panama. Carapace light brown with darker streaks. Sternum black. Coxae and distal articles of legs light brown. Dorsum of abdomen white, tips of spines black; sides and venter with black marks. Carapace with indistinct light rim and one pair of shallow dimples in grooves between head and thorax. Thorax very high, with distinct tho-

racic mark (Fig. 253). Abdomen with five pairs of spines, the third very small, the fourth largest (Figs. 252, 253). Total length, 9.7 mm. Carapace, 3.8 mm long, 3.0 mm wide. First femur, 4.9 mm; patella and tibia, 4.8 mm; metatarsus, 3.7 mm; tarsus, 1.2 mm. Second patella and tibia, 4.3 mm; third, 2.4 mm. Fourth femur, 6.2 mm; patella and tibia, 5.2 mm; metatarsus, 4.1 mm; tarsus, 1.3 mm.

Male. Carapace orange, sides darker. Labium and endites orange, sternum shiny black. Coxae light orange, distal articles of legs orange. Dorsum of abdomen white and black (Fig. 258); venter with median longitudinal band on genital area, a line of indistinct black marks on each side, and black mark behind spinnerets, widest posteriorly. First coxa with hook. Abdomen rounded behind, sides almost parallel (Fig. 258). Total length, 4.3 mm. Carapace, 1.9 mm long, 1.5 mm wide. First femur, 1.7 mm; patella and tibia, 1.6 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm. Second patella and tibia, 1.3 mm; third, 0.7 mm. Fourth femur, 1.9 mm; patella and tibia, 1.5 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm.

Variation. Females vary in total length from 8.2 to 10.6 mm. The small third pair of spines may be absent. The legs of females from Panama are longer than those of females from Peru: length of first patella-tibia in those from Panama is 1.6 times carapace width; in those from Peru about 1.4 times carapace width. Also, Peruvian specimens appear to be more sclerotized. They have some additional small sclerotized disks on the dorsum, and the light area on the posterior of the epigynum is smaller. The specimen from Bolivia has longer spines and the epigynum has a longer lobe.

Note. The male was not collected with the female, but came from an area where females have been collected (Huánuco Prov., Peru), and has a similar black sternum. The association is uncertain.

Diagnosis. Micrathena macfarlanei can be separated from others of the *kirbyi* group by having eight to ten pairs of spines, and by their arrangement (Figs. 252, 253). It differs from *M. armigera* and *M. kirbyi* by usually having a light patch on the posterior of the epigynum (Fig. 256). It differs from *M. armigera* by having endites, labium and sternum black, by having the second and third pairs of spines on the abdomen shorter (Figs. 252, 253), and by the longer, pointed lobe of the epigynum (Figs. 254, 255). It lacks the abdominal markings of *M. kirbyi.* The black sternum and the rugose, pointed base of the median apophysis of the palpus (Figs. 259, 260) separate the male from related species.

Distribution. Panama to Bolivia and southern Brazil (Map 5).

Records. PANAMA: *Panamá Prov.* Barro Colorado Isl., canal area, July 1936, ♀, June 1939, 2 imm. (A. M. Chickering, MCZ). PERU: *Dept. Huánuco.* Tingo María, 8 Oct. 1946, ♀ (J. C. Pallister, AMNH), 670 m, Dec. 1946, 6♀, 1 imm. (W. Weyrauch, AMNH); Cucharas, Feb.–Apr. 1954, 2♀, 1 imm. (F. Woytkowski, EPC); Aucayacu, 1 June 1967, ♂ (A. F. Archer, AMNH). BRAZIL: *Est. Amazonas.* mouth of Rio Embira and Rio Jurua, 1933, ♀ (B. A. Krukoff, AMNH). *Bahia.* Uruçuca, 27 Nov. 1977, ♀ (J. S. Santos, FZRS); Camacari, 14 Oct. 1978, ♀ (J. S. Santo, FZRS). *Rio de Janeiro.* Guitacazes, ♀ (M. Rosa, MNRJ). *São Paulo.* Diadema (Eldorado), 12 May 1962, ♂ (F. Lane, MZSP). BOLIVIA: *Dept. La Paz.* Coroico, ♀ (E. Reimoser, MCZ).

Micrathena armigera (C. L. Koch)
Figures 261–265; Map 5

Acrosoma armigera C. L. Koch, 1838: 11, fig. 257, ♀. Female specimen from Brazil, from the collection of Jakob Sturm, probably in the ZSM, destroyed.

Micrathena armigera:—Roewer, 1942: 954. Bonnet, 1957: 2862 (not Reimoser, 1917).

Name. Koch's illustration shows a carapace perhaps with dimples, not present on specimens nor in Koch's description.

Description. Female. Carapace orange, sides of thorax dark brown. Sternum dark orange, coxae orange, legs dark orange.

Dorsum of abdomen whitish with orange spines and orange disks; venter with sclerotized areas dark orange. Carapace with rim and thoracic depression; no dimples. Abdomen with ten spines (Fig. 262). Total length, 11.0 mm. Carapace, 3.6 mm long, 3.0 mm wide. First femur, 4.2 mm; patella and tibia, 4.2 mm; metatarsus, 3.0 mm; tarsus, 1.2 mm. Second patella and tibia, 3.7 mm; third, 2.1 mm. Fourth femur, 5.0 mm; patella and tibia, 4.3 mm; metatarsus, 2.7 mm; tarsus, 1.3 mm.

Diagnosis. *Micrathena armigera* differs from *M. kirbyi* by its orange coloration and by lacking the black markings of the abdomen. The epigynum differs by having the transverse bar more posterior (Fig. 263). The epigynum differs from that of *M. macfarlanei* by having a tiny lobe (Fig. 263) with a transverse ridge behind, visible in posterior view (Fig. 264).

Variation. Females vary in total length from 10.5 to 12.2 mm.

Note. The male is unknown.

Distribution. Amazon area (Map 5).

Records. GUYANA: 1913, ♀ (Parrish, CUC). PERU: *Dept. Loreto.* Iquitos, ♀ (MCZ). BRAZIL: *Est. Pará.* Canindé, Feb.–May 1964, 2♀ (J. Carvalho, AMNH); km 305, Rodovia Belém-Brasília, 3°10′S, 47°30′W, ♀ (E. Dante, MZSP).

Micrathena kirbyi (Perty)
Figures 266–270; Map 5

Acrosoma kirbyi Perty, 1833: 195, pl. 38, fig. 11. Female holotype from Sebastianopolis [Rio de Janeiro] (ZSM), destroyed in the last war.

Acrosoma oblonga Taczanowski, 1872: 275, pl. 6, fig. 26, ♀. Female holotype from Cayenne, French Guiana (PAN), examined.

Micrathena oblonga:—Petrunkevitch, 1910: 213, pl. 21, figs. 12, 13, ♀.

Micrathena kirbyi:—Reimoser, 1917: 135, pl. 9, fig. 26, ♀. Roewer, 1942: 959. Bonnet, 1957: 2871.

Description. Female. Carapace, sternum, legs blackish brown, except coxae and femora, orange. Dorsum of abdomen boldly marked in black and white with transverse black marks; sides mostly black with some white marks (Figs. 266, 267); venter black with a white patch each side of epigastric area, two white spots on each side of spinnerets, and a median white spot behind spinnerets. Carapace with rim, a round thoracic mark; thorax high (Fig. 267). Sides of abdomen almost parallel, with ten spines (Fig. 267). Total length, 11.0 mm. Carapace, 3.9 mm long, 3.2 mm wide. First femur, 4.6 mm; patella and tibia, 4.7 mm; metatarsus, 3.5 mm; tarsus, 1.0 mm. Second patella and tibia, 4.1 mm; third, 2.4 mm. Fourth femur, 6.3 mm; patella and tibia, 5.1 mm; metatarsus, 4.2 mm; tarsus, 1.3 mm.

Variation. Females vary in total length from 8.3 to 12.9 mm. The tiny third pair of spines of the abdomen may be absent. The T-shaped tip of the epigynum is more variable in shape than that of other species.

Note. The male is unknown. Juvenile males have a black head, a black patch on each side of the carapace and on each side of the anterior of the abdomen. The sternum is black, coxae light; there is a median black band from anterior to posterior on the abdomen. The abdomen is as wide posteriorly as anteriorly, slightly convex on each side. Total length is 4.5 mm.

Diagnosis. *Micrathena kirbyi* is one of the largest species of the *M. kirbyi* group.

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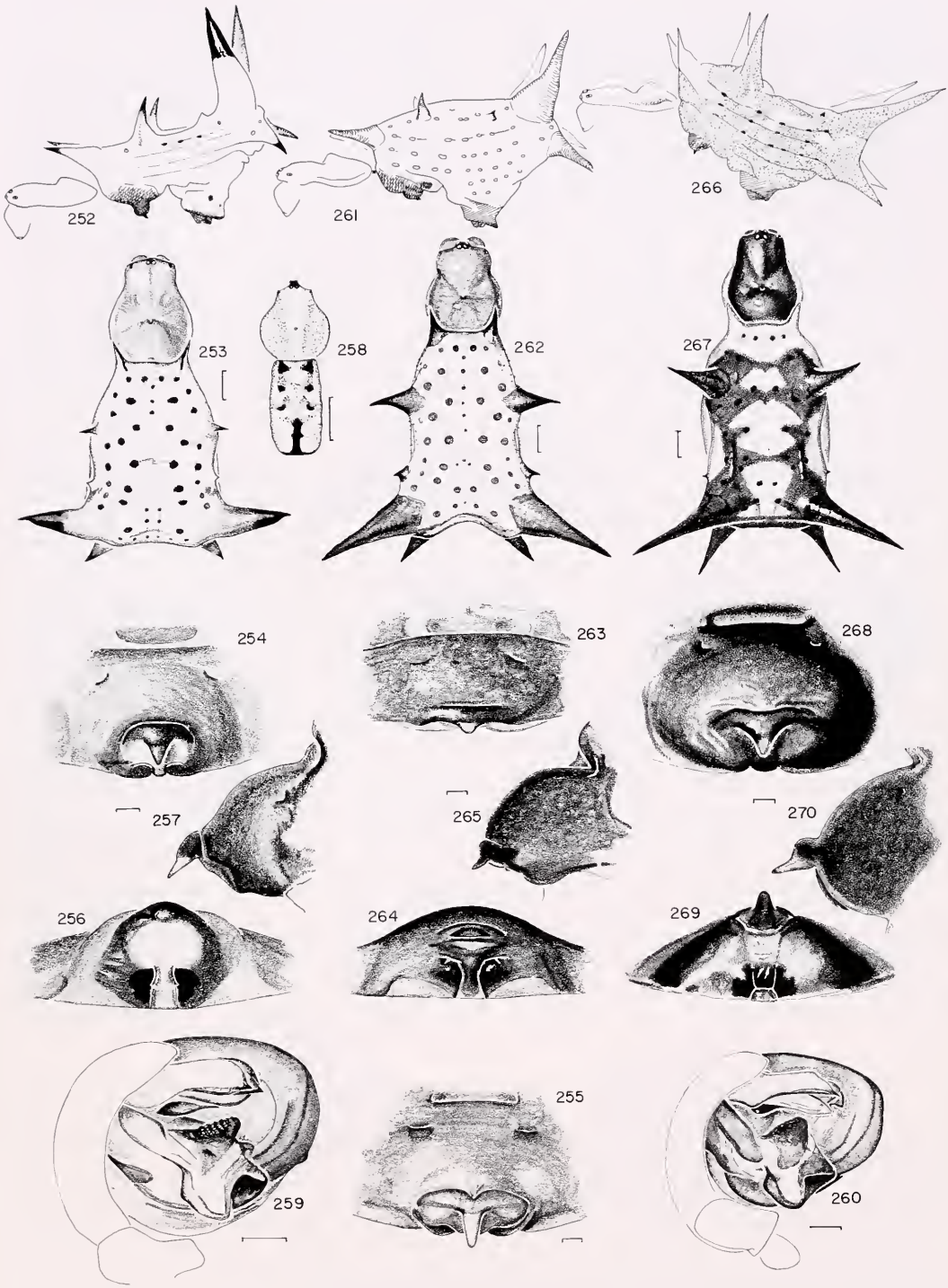
Figures 252–260. *Micrathena macfarlanei* Chickering. 252–257. Female. 252. Lateral. 253. Dorsal. 254, 255. Epigynum, ventral. 256. Epigynum, posterior. 257. Epigynum, lateral. 254, 256, 257. (Panama). 255. (Bolivia). 258–260. Male. 258. Dorsal. 259, 260. Left male palpus, mesal. 259. (Peru). 260. (São Paulo, Brazil).

Figures 261–265. *Micrathena armigera* (C. L. Koch), female. 261. Lateral. 262. Dorsal. 263. Epigynum, ventral. 264. Epigynum, posterior. 265. Epigynum, lateral.

Figures 266–270. *Micrathena kirbyi* (Perty), female. 266. Lateral. 267. Dorsal. 268. Epigynum, ventral. 269. Epigynum, posterior. 270. Epigynum, lateral.

Scale lines. 0.1 mm, except Figures 252, 253, 258, 261, 262, 266, 267, 1.0 mm.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It differs from *M. miles* by having a small pair of light spines overhanging the carapace (Fig. 267). It differs from the other eight- to ten-spined species by the bold markings and by having a light patch on the posterior of the epigynum dorsal to the lobe. The light area has a black patch on each side dorsally (Fig. 269).

Natural History. The species has been collected in forest.

Distribution. Amazon (Map 5).

Records. COLOMBIA; *Dept. Meta.* Villavicencio, ♀ (AMNH). *Caqueta.* Río Orteguaza, 4♀ (AMNH). *Amazonas.* Leticia, ♀ (AMNH). *Vaupés.* Río Vaupés, ♀ (AMNH). VENEZUELA: *Est. Bolivar.* Kavanayen, ♀ (EMUC). GUYANA: *Essequibo Prov.* Rockstone, ♀ (AMNH); Kaieteur, ♀ (AMNH); Kuyuwini Land, Kuyuwini River, ♀ (AMNH). Canister Falls, ♀ (BMNH). SURINAME: *Saramacca Prov.* Voltzberg-Raleighvallen Nature Reserve, ♀ (MCZ); Coppename Riv., 2♀ (AMNH). *Suriname.* Paramaribo, ♀ (AMNH), ♀ (NMW). Upper Suriname River, ♀ (BMNH). PERU: *Dept. Loreto.* upper Río Utoquinia, ♀ (AMNH). BRAZIL: *Est. Pará.* Belém, 12♀, 9 imm. (ZMSP, CAS, MEG, MCZ); Canindé, 17♀ (AMNH); 50 km E of Canindé, 2♀ (AMNH); Rio Gurupi, 2♀ (MZSP); Cachoeira, imm. (IBSP). *Amazonas.* mouth of Rio Embira, Rio Jurua, ♀ (MCZ); Manaus, ♀ (INPA), ♀ (FAM); Utinga, ♀ (MZSP). *Acre.* Rio Alto Purus, W. Sena Madureira, 2♀ (MCZ). *Rondônia.* Vila Murtinho, 5♀ (MCZ), 2♀ (MCZ). *Mato Grosso.* Aripuaná, ♀ (MCZ); Chapada dos Guimarães, ♀ (AMNH); Reserva Humboldt, ♀ (INPA).

Micrathena lindenbergi Mello-Leitão
Figures 271–275; Map 5

Micrathena lindenbergi Mello-Leitão, 1940: 208. Female holotype from Colatina [Est. Espírito Santo, Brazil] (no. 55553 MNRJ), lost.

? *Micrathena parallela* Mello-Leitão, 1940: 209. Male holotype from Colatina, Santo Espirito (no. 58346, MNRJ), lost. Name preoccupied by *M. parallela* (O. P.-Cambridge). DOUBTFUL NEW SYNONYMY.

? *Micrathena sanctispiritus* Brignoli, 1983: 249. New name for *M. parallela* Mello-Leitão, name preoccupied. DOUBTFUL NEW SYNONYMY.

Synonymy. Six females from Goitacazes in the Museu Nacional, Rio de Janeiro had been labeled by Mello-Leitão as being this species.

Mello-Leitão did not illustrate *M. parallela.* The name was applied to a large male, 6.5 mm total length, having the abdomen three times as long as wide. It came from the same locality as *M. lindenbergi* and may have been collected with it.

Description. Female. Carapace dark brown with some light orange posteromedially. Sternum orange. Coxae orange with some black spots. Legs brown. Dorsum of abdomen black and white; sides black; venter orange in middle, black on each side; some white pigment behind on each side of spinnerets. Carapace with three pairs of dimples, a distinct thoracic depression, narrow rim and high thorax (Figs. 271, 272). Abdomen with ten spines; abdomen length more than twice width. Total length, 9.6 mm. Carapace, 3.0 mm long, 2.4 mm wide. First femur, 3.3 mm; patella and tibia, 3.4 mm; metatarsus, 2.2 mm; tarsus, 1.2 mm. Second patella and tibia, 2.6 mm; third, 1.7 mm. Fourth fe-

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Figures 271–275. *Micrathena lindenbergi* Mello-Leitão, female. 271. Lateral. 272. Dorsal. 273. Epigynum, ventral. 274. Epigynum, posterior. 275. Epigynum, lateral.

Figures 276–282. *Micrathena stuebeli* (Karsch). 276–280. Female. 276. Lateral. 277. Dorsal. 278. Epigynum, ventral. 279. Epigynum, posterior. 280. Epigynum lateral. 281, 282. Male. 281. Dorsal. 282. Left palpus, mesal.

Figures 283–289. *Micrathena guanabara* n. sp. 283–287. Female. 283. Lateral. 284. Dorsal. 285. Epigynum, ventral. 286. Epigynum, posterior. 287. Epigynum, lateral. 288, 289. Male. 288. Dorsal. 289. Male palpus, mesal.

Scale lines. 0.1 mm, except Figures 271, 272, 276, 277, 281, 283, 284, 288, 1.0 mm.

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mur, 4.2 mm; patella and tibia, 3.3 mm; metatarsus, 2.4 mm; tarsus, 1.0 mm.

Diagnosis. Micrathena lindenbergi differs from *M. agriliformis* and *M. pupa* by the anterior spines on the abdomen (Figs. 271, 272). It differs from *M. guanabara* by the worm-shaped, posteriorly constricted abdomen (Fig. 272).

Distribution. Eastern Brazil (Map 5).

Records. BRAZIL: *Est. Bahia.* Camacari, 14 Oct. 1978, ♀ (J. S. Santos, FZRS). *Espírito Santo.* Rio São José, Sept. 1942, 4♀ (H. Soares, MZSP). *Rio de Janeiro.* Goitacazes, 6♀ (M. Rosa, MNRJ). *Minas Gerais.* Rio Matipoó, Sept. 1919, ♀ (P. Fonseca, MZSP). *Paraná.* Engenheiro Lange, April 1946, ♀ (MZSP).

Micrathena stuebeli (Karsch)
Figures 276–282; Map 5

Acrosoma stübeli Karsch, 1886: 340. Female holotype from Bogotá, Colombia (ZMB), examined.
Micrathena spathulifera Simon, 1895: 852, fig. 912, ♀. Female from Loja, Ecuador (no. 7831, MNHN), examined. First synonymized by Reimoser, 1917.
Micrathena stübeli:—Reimoser, 1917: 118, pl. 6, fig. 17, ♀. Roewer, 1942: 964.
Micrathena stuebeli:—Bonnet, 1957: 2879.

Type. The holotype of *M. stuebeli* has been pinned through the anterior part of the abdomen. It had been placed in alcohol before loaning, but is in poor condition, almost devoid of color.

Description. Female. Carapace, sternum dark brown. Legs dark brown, except for light coxae and proximal ends of femora. Abdomen white in middle of dorsum; black patches on sides; posterior sclerotized area dark brown; venter black. Sides of abdomen with some white patches on underside of folds. Carapace with very high thorax and a deep transverse groove (Fig. 276). Abdomen wider than long, with 12 spines, the fourth and fifth form a double spine, the anterior of which has a posterior lobe. Entire posterodorsal region of abdomen sclerotized (Figs. 276, 277). Total length, 8.8 mm. Carapace, 3.2 mm long, 2.7 mm wide. First femur, 3.1 mm; patella and tibia, 3.2 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm. Second patella and tibia, 2.9 mm; third, 1.7 mm. Fourth femur, 3.4 mm; patella and tibia, 2.9 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm.

Male. Carapace dark brown; sternum light brown. Legs brown, first two femora darkest. Dorsum of abdomen brown with white pigment spots along sides and a pair in middle; venter black. Carapace slightly rugose with distinct thoracic depression; no dimples. First coxa with hook; second femur with groove. Sides of abdomen almost parallel, widest in middle; posterior edge with three folds (Fig. 281). Total length, 5.2 mm. Carapace, 2.3 mm long, 1.5 mm wide. First femur, 1.8 mm; patella and tibia, 1.8 mm; metatarsus, 1.1 mm; tarsus, 0.6 mm. Second patella and tibia, 1.6 mm; third, 0.9 mm. Fourth femur, 1.9 mm; patella and tibia, 1.6 mm; metatarsus, 1.2 mm.

Variation. Females vary in total length from 7.1 to 8.9 mm. The smallest specimen from Zamora had only the spines on the posterior of the abdomen sclerotized. The female from Ambato had lobes behind each one of the four lateral spines.

Note. The male has not been collected with the female, but was collected in an area where females have been found. The palpus is slightly expanded and transparent. The cymbium has been drawn in, for ease of comparison, as if the palp were contracted.

Diagnosis. Micrathena stuebeli female differs from *M. digitata* found in Brazil by having a pair of anterior spines overhanging the carapace (Figs. 276, 277), and by the posterior aspect of the epigynum (Fig. 279). It differs from others by the wide abdomen having a lobed spine (Fig. 277).

The male differs from others by having the distal margin of the median apophysis changed into a spine (Fig. 282).

Distribution. Colombia and Ecuador (Map 5).

Records. ECUADOR: *Prov. Pichincha.* Sierra Inca, 2♀ (NMW). *Napo.* Río Hollin, 600 m, Jan. 1985, ♀ (G. Moreion, MECN). *Tungurahua.* Ambato, 2♀ (AMNH); Tungurahua, 2,600 m, 6 May 1979, ♂ (W.

Clarke-MacIntyre, AMNH). *Morona Santiago.* nr. General Plaza (Limón), 1977, ♀ (N. Engler, MCZ). *Loja.* Zamora, 1,800–2,200 m, 28 Oct. 1977, ♀ (L. Peña, AMNH).

Micrathena guanabara new species
Figures 283–289; Map 5

Holotype. Female and male paratype from Rio de Janeiro, Brazil, 29 Jan. 1945 (P. Wygodzinsky, no. 7932, MZSP). The specific name is a noun in apposition after Guanabara Bay.

Description. Female. Carapace dark brown and black with dark color emphasizing sculpturing, lightest in areas between dimples. Sternum orange. Coxae lighter orange; distal articles of legs orange-brown. Dorsum of abdomen white with black spines, except for large posterolateral spines, which are black distally; sclerotized spots orange-brown; venter whitish, with book-lung covers and ring around spinnerets black; white patches on sides. Carapace with distinct rim and median thoracic depression, and three pairs of very large dimples in grooves. Posterior median eyes slightly larger than others, which are subequal. Abdomen longer than wide, with ten spines: first pair overhanging carapace; third pair, posterolaterals, largest (Figs. 283, 284). Total length, 8.3 mm. Carapace, 3.2 mm long, 2.4 mm wide. First femur, 3.4 mm; patella and tibia, 3.6 mm; metatarsus, 2.5 mm; tarsus, 1.1 mm. Second patella and tibia, 3.1 mm; third, 2.0 mm. Fourth femur, 4.3 mm; patella and tibia, 3.5 mm; metatarsus, 2.9 mm; tarsus, 1.1 mm.

Male. Carapace black with two orange patches, a transverse one in front of thoracic depression, and a longitudinal one behind. Chelicerae black, sternum orange. Legs dusky orange. Dorsum of abdomen with white pigment on sides and gray pigment (Fig. 288); venter orange between black book-lung covers, orange behind and black on sides; black behind spinnerets with orange sides. Carapace with very distinct dimples and thoracic depression. Posterior median eyes 1.3 diameters of anteriors; laterals 0.8 diameters of anterior median eyes. Coxal hook present. First patella and tibia with macrosetae. Abdomen rectangular, longer than wide (Fig. 288). Total length, 6.6 mm. Carapace, 2.4 mm long, 1.7 mm wide. First femur, 2.2 mm; patella and tibia, 2.2 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm. Second patella and tibia. 1.8 mm; third, 1.1 mm. Fourth femur, 2.7 mm; patella and tibia, 2.2 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm.

Variation. Females vary in total length from 8.0 to 9.0 mm, males from 6.0 to 6.6 mm. The width and length of the lobe of the epigynum is slightly variable.

Notes. The holotype was collected with a male; the coloration indicates that they belong together.

There is a specimen of this species from Brazil in the Berlin Museum, originally pinned, which is marked "*M. crassispina.*"

Diagnosis. This species differs from *M. crassispina* in having an additional pair of spines on the posterior slope of the abdomen (Figs. 283, 284). The large dimples and grooves of the carapace separate this species from others of this species group. The male differs from *M. lindenbergi* by having a long, rectangular abdomen, and by the distinctly shaped conductor (Fig. 289).

Distribution. State of Rio de Janeiro, Brazil (Map 5).

Paratypes. BRAZIL: *Est. Rio de Janeiro.* Ilha Grande, 4 Sept. 1944, ♀ (H. Sick, AMNH); Sumaré, Feb. 1946, ♀ (H. Sick, AMNH); Jacarépaguá, 2♀ (MNRJ); Niterói, ♀ (MNRJ); Rio de Janeiro, 26 May 1979, 2♀, ♂ (C. J. Becker, FZRS), ♀ (ZMK).

Micrathena duodecimspinosa (O. P.-Cambridge)
Figures 290–303; Map 6

Acrosoma 12-spinosum O. P.-Cambridge, 1890: 63, pl. 8, fig. 12, ♀. Female holotype and 14 paratypes from Bugaba, Panama (BMNH), examined. Keyserling, 1892: 18, pl. 1, fig. 14. F. P.-Cambridge, 1904: 535, pl. 5, fig. 18, ♀.

Micrathena duodecimspinosa:—Reimoser, 1917: 108,

pl. 5, fig. 12, ♀. Roewer, 1942: 957. Bonnet, 1957: 2866. Chickering, 1961: 408, figs. 41–45, ♀ (not male).

Micrathena subspinosa F. P.-Cambridge, 1904: 535, pl. 51, fig. 17, ♀. Female holotype from Ayutla, Guatemala (BMNH), examined. Reimoser, 1917: 115. Roewer, 1942: 964. Bonnet, 1957: 2880. Chickering, 1961: 463, figs. 194–197. NEW SYNONYMY.

Micrathena disjuncta Chickering, 1961: 403, figs. 26–30, ♂. Male holotype from Barro Colorado Island, Panama (MCZ), examined. NEW SYNONYMY.

Micrathena macilenta Chickering, 1961: 432, figs. 103–109, ♂. Male holotype from Barro Colorado Island, Panama (MCZ), examined. NEW SYNONYMY.

Synonymy. The epigynum of the holotype of *A. duodecimspinosum* is weakly sclerotized, either just before or just after the last molt. It has not been illustrated here; the dorsum of the female has (Fig. 294).

Chickering was not certain that *M. subspinosa* was a separate species from *M. duodecimspinosa*. I believe they are the same, despite the drawn-out, triple posterolateral spines and the posteriormost spine being farther from the other two spines (Fig. 295).

Micrathena disjuncta and *M. macilenta* are the male of *M. duodecimspinosa*. Chickering illustrated and perhaps examined the two males from slightly different angles. Also, the type of *M. disjuncta* has just molted and is not sclerotized; the abdomen is shorter and wider than the sclerotized type of *M. macilenta*. Chickering thought that males he had collected in Boquete, Chiriquí Mountains belonged to *M. duodecimspinosa*. They are not this species, since no females have been collected in the mountains; they are *M. lucasi*.

Description. Female. Carapace orange, brown on each side of thorax. Sternum, legs brown. Dorsum of abdomen white in center, blackish on each side; anterior, posterior spines orange; venter dark brown with paired white spots, a large white patch on each side of spinnerets and white median band from behind spinnerets up posterior. Carapace with dimples and high thorax (Figs. 290–295). Total length, 6.2 mm. Carapace, 2.2 mm long, 1.9 mm wide. First femur, 2.3 mm; patella and tibia, 2.4 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm. Second patella and tibia, 2.2 mm; third, 1.3 mm. Fourth femur, 2.6 mm; patella and tibia, 2.0 mm; metatarsus, 1.5 mm; tarsus, 0.6 mm.

Male holotype of *M. disjuncta*. Carapace yellow-white, black on each side. Sternum, legs yellow-white. Dorsum of abdomen white with black marks; sides black, venter gray. Carapace with thoracic mark. First and second legs have macrosetae. First coxa with hook, second femur with groove. Abdomen almost rectangular, very slightly lobed on sides (Fig. 302). Total length, 3.8 mm. Carapace, 1.7 mm long, 1.2 mm wide. First femur, 1.6 mm; patella and tibia, 1.6 mm; metatarsus, 1.0 mm; tarsus, 0.4 mm. Second patella and tibia, 1.2 mm; third, 0.7 mm. Fourth femur, 1.7 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 4.9 to 7.6 mm. The carapace of females has one to three pairs of dimples. The abdomen always has 12 spines (one pair overhanging carapace, two pairs on sides, and three with a joint socket posterolaterally), but is quite variable in outline (Figs. 290–295). The transverse bar of the epigynum may lack a posterior median lobe; it may be broken off (Figs. 297, 299, 301).

Note. Males and females have been col-

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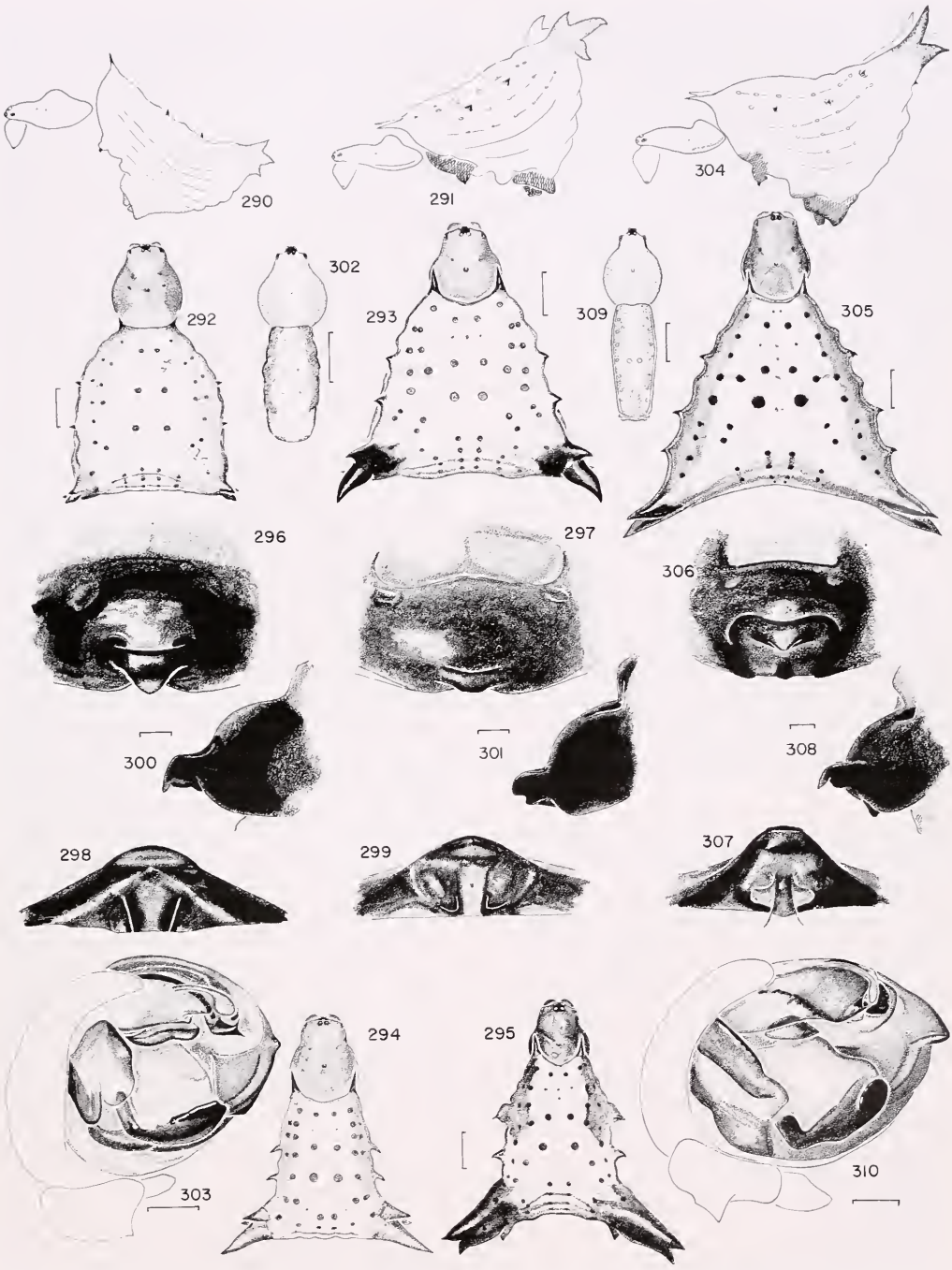
Figures 290–303. *Micrathena duodecimspinosa* (O. P.-Cambridge). 290–301. Female. 290, 291. Lateral. 292–295. Dorsal. 290, 292. (Barro Colorado Island, Panama). 291, 293. (Osa Peninsula, Costa Rica). 294. (Bugaba, Panama). 295. (Guatemala). 296, 297. Epigynum, ventral. 298, 299. Epigynum, posterior. 300, 301. Epigynum, lateral. 296, 298, 300. With lobe. 297, 299, 301. Lobe torn off. 302, 303. Male. 302. Dorsal. 303. Left palpus, mesal.



Figures 304–310. *Micrathena parallela* (O. P.-Cambridge). 304–308. Female. 304. Lateral. 305. Dorsal. 306. Epigynum, ventral. 307. Epigynum, posterior. 308. Epigynum, lateral. 309, 310. Male. 309. Dorsal. 310. Palpus, mesal.

Scale lines. 0.1 mm, except Figures 290–295, 302, 304, 305, 309, 1.0 mm.

lected together on Barro Colorado Island, Panama canal area, and a male was found in Bugaba, the type locality of *M. duodecimspinosa*. The male is similar to the one of *M. plana*, a related species.

Diagnosis. This species is very similar to *M. plana*, but apparently differs by always having anterior edge of the transverse bar of the epigynum concave (Fig. 296, 297). The male differs by having a radix with an upper lobe (on cymbial margin left of center in Fig. 303).

Distribution. Guatemala to southern Colombia (Map 6).

Records. COSTA RICA: *San José Prov.* San José, ♀ (M. Valerio, MCZ); La Caja, San José, 1930, ♀ (Schmidt, NMW). *Puntarenas.* 4 km SW Rincón, March 1967, ♀; 2.5 km SW Rincón, March 1967, ♀ (OTS course, MCZ); Río Jesus María, 5♀ (Biolley, Tristan, MCZ). PANAMA: *Bocas de Toro Prov.* Bugaba, ♂ (Champion, BMNH). *Panamá.* Barro Colorado Island, Gatún Lake, many collections, ♀, ♂ (AMNH, MCZ, MZSP); France Field, Canal area, Aug. 1938, ♀ (A.M. Chickering, MCZ). COLOMBIA: *Dept. Nariño.* Barbacoas, 20 m, 20 March 1974, ♀ (W. Eberhard, MCZ).

Micrathena parallela (O. P.-Cambridge)
Figures 304–310; Map 6

Acrosoma parallela O. P.-Cambridge, 1890: 60, pl. 8, fig. 15, ♂. Male lectotype, two male paralectotypes (and parts of a male paralectotype which is *M. duodecimspinosa*) from Bugaba, Panama (BMNH), examined. Keyserling, 1892: 6, pl. 1, fig. 12, ♂.

Micrathena parallela:—F. P.-Cambridge, 1904: 533, pl. 50, fig. 13, ♂. Roewer, 1942: 960. Bonnet, 1957: 2873. Chickering, 1961: 443, figs. 133–137, ♂.

Micrathena serrata F. P.-Cambridge, 1904: 534, pl. 50, fig. 19, ♀. Seventeen female syntypes from Volcán de Chiriquí, Panama (BMNH), examined. Reimoser, 1917: 114. Roewer, 1942: 963. Bonnet, 1957: 2877. Chickering, 1961: 455, figs. 169–173, ♀. NEW SYNONYMY.

Synonymy. Micrathena serrata is the female of *M. parallela*.

Description. Female from Panama. Carapace orange, gray on sides. Sternum orange-brown. Legs brown. Dorsum of abdomen white, with a dark band on each side (Fig. 305); spines orange-brown; sides of abdomen dark with dorsoventral rows of white patches; venter dark. Carapace with high thorax and narrow rim, three pairs of small dimples and a median thoracic mark (Figs. 304, 305). Total length, 7.4 mm. Carapace, 2.4 mm long, 2.2 mm wide. First femur, 2.4 mm; patella and tibia, 2.6 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm. Second patella and tibia, 2.3 mm; third, 1.4 mm. Fourth femur, 2.7 mm; patella and tibia, 2.2 mm; metatarsus, 1.7 mm; tarsus, 0.6 mm.

Male from Panama. Carapace dark dusky orange, sides slightly darker. Sternum dark orange, legs dusky orange. Dorsum of abdomen whitish orange with five gray patches, four anterolateral and one posteromedian, all with indistinct outline; venter blackish. Sides of thorax slightly rugose, with a distinct round thoracic depression and indistinct tubercles. A hook on first coxa, a groove on second femur. Sides of abdomen nearly parallel, with two folds on posterior margin (Fig. 309). Total length, 5.2 mm. Carapace, 1.9 mm long, 1.5 mm wide. First femur, 1.7 mm; patella and tibia, 1.7 mm; metatarsus, 1.1 mm; tarsus, 0.5 mm. Second patella and tibia, 1.4 mm; third, 0.9 mm. Fourth femur, 1.8 mm; patella and tibia, 1.4 mm; metatarsus, 1.1 mm.

Variation. Females vary in total length from 6.2 to 8.0 mm. The dimples on the female carapace may be indistinct. Sometimes there is an additional pair of spines between the second and third pair on the abdomen, giving the abdomen 16 spines. The spines on the posterior of the abdomen are usually minute.

Note. Four males were collected with an equal number of females by W. J. Gertsch at Volcán, Panama.

Diagnosis. This species has a distinct epigynum: the anterior margin of the transverse bar surrounds and frames the sides (Fig. 306). In posterior view there is a median dark septum with a semicircular

lateral groove on each side (Fig. 307). There are usually three teeth on the sides of the abdomen: a posterolateral double spine and a minute spine toward the middle on the posterior. The outline of the tegulum of the male palpus, with a lobe distally on the venter, is diagnostic (Fig. 310).

Distribution. Mountains of Costa Rica and Panama (Map 6).

Records. COSTA RICA: *San José Prov.* La Verbena, 2♀ (Tristan, MCZ); San Antonio de Escazú, 1,350 m, Oct. 1980, ♀ (W. Eberhard, MCZ). *Puntarenas.* Monteverde Forest Reserve, 1,580 m, 22 Nov. 1977, ♀ (C. L. Craig, MCZ), ♀ (C. W. Palmer, AMNH). PANAMA: *Chiriquí Prov.* Volcán, Aug. 1950, 9♀ (A. M. Chickering, MCZ), Feb. 1936, 4♀, 4♂, 13 imm. (W. J. Gertsch, AMNH); Cerro Punta, June 1962, 2♀ (R. Zweifel, AMNH).

Micrathena plana (C. L. Koch) Figures 311–325; Map 6

Acrosoma planum C. L. Koch, 1836: 81, fig. 228, ♀. Female holotype from Brazil (ZSM), destroyed in the last war.

? *Plectana alata* Walckenaer, 1841: 193. Female from Santa Catarina, Brazil, lost. NEW DOUBTFUL SYNONYMY.

Acrosoma maronica Taczanowski, 1873: 272, pl. 6, fig. 24, ♀. Two female syntypes from Saint Laurent de Maroni, French Guyana (PAN), examined. NEW SYNONYMY.

Micrathena pubescens:—Simon, 1895: 854. Male paralectotype, not female lectotype.

Micrathena maronica:—Reimoser, 1917: 106. Roewer, 1942: 960. Bonnet, 1957: 2871.

Micrathena plana:—Reimoser, 1917: 109. Roewer, 1942: 961. Bonnet, 1957: 2874.

Micrathena nitida Chickering, 1964: 272, figs. 51–56, ♂. Male holotype from near Port of Spain, Trinidad, Lesser Antilles (MCZ), examined. NEW SYNONYMY.

Synonymy. Taczanowski named the species *A. maronica,* and Chickering described the male as *M. nitida. Plectana alata* Walckenaer might be this species; it has two posterior lobes and twelve spines.

Description. Female. Carapace, legs olive brown. Sternum dark brown. Dorsum of abdomen white with gray band on each side; sides and venter dark with pairs of white patches. Carapace with an indistinct pair of dimples, a thoracic mark and high thorax; lacking rim. Abdomen with two anterior spines, two thorns on each side of dorsum with a swelling in between, and a posterolateral spine with three tips, the middle one largest (Figs. 311–314). Total length, 5.5 mm. Carapace, 2.2 mm long, 1.8 mm wide. First femur, 2.2 mm; patella and tibia, 2.2 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm. Second patella and tibia, 1.9 mm; third, 1.2 mm. Fourth femur, 2.4 mm; patella and tibia, 1.9 mm; metatarsus, 1.4 mm; tarsus, 0.6 mm.

Male. Color like female. Carapace with median thoracic mark; without rim or dimples. First coxa with small lateral hook; groove on second femur. First and second legs with macrosetae. Abdomen longer than wide, narrowing posteriorly, with small fold below each posterior lateral tip (Fig. 324). Total length, 4.5 mm. Carapace, 1.7 mm long, 1.4 mm wide. First femur, 1.4 mm; patella and tibia, 1.3 mm; metatarsus, 0.8 mm; tarsus, 0.4 mm. Second patella and tibia, 1.0 mm; third, 0.7 mm. Fourth femur, 1.5 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 4.3 to 6.1 mm, males from 3.8 to 5.4 mm. Some females have a minute pair of teeth on the posterior face of the abdomen; some have minute denticles in front of the first lateral spines. A single specimen from the Virgin Islands had an almost flat, sclerotized plate in place of the lateral spines. Some females and a male from Venezuela have the dorsum of the abdomen all black. In some females the convex anterior edge of the transverse bar of the epigynum has disappeared (Fig. 317). In some the transverse bar has a lobe (Fig. 315); in others it has almost disappeared. Some females might belong to other similar, related species. Also, the females which have some characteristics of *M. triangularis* (see below) suggest that the species hybridize.

Note. Males and females have been collected together in Colombia, Venezuela, Ecuador, and Brazil.

Diagnosis. The female differs from *M. triangularis* and other species with 12 to 16 (rare) spines by having a convex anterior edge on the swollen transverse bar, and by its diminished (or absent) posterior lobe (Figs. 315–317). Females differ from *M. triangularis* by the abdomen usually having only two spines on the sides, separated by a lobe (Fig. 312). The related *M. duodecimspinosa* has the anterior margin of the transverse bar concave. The narrowed posterior of the male abdomen (Fig. 324) is diagnostic, as is the curved embolus visible above the terminal apophysis (Fig. 325). The terminal apophysis has an appendage which hangs over the conductor (Fig. 325).

Natural History. The species has been found in gallery forest in Mato Grosso and is found at low elevations.

Distribution. Panama, Virgin islands, Trinidad, Colombia to Argentina (Map 6).

Records. PANAMA: *Chiriquí Prov.* David, Dec. 1946, ♂ (N. L. H. Krauss, AMNH). VIRGIN ISLANDS: *St. John.* Bordeaux Mtn., 17 Dec. 1965, ♀ (Isl. Project staff, AMNH). TRINIDAD: common, ♀, ♂ (AMNH, MCZ). VENEZUELA: *Est. Delta-Amacuro.* Río Orinoco delta, ♀ (MCZ). *Monagas.* Caripito, ♀ (AMNH). *Miranda.* Maracay, 2♀ (MCZ). *Carabobo.* San Esteban, ♀♀, ♂♂ (CUC). GUYANA: *Essequibo Co.* nr. Tacuto, 2♀ (AMNH); Isherton, ♀ (AMNH). SURINAME: *Suriname Prov.* Paramaribo, ♂ (AMNH). *Marowijn.* Langaman, ♀ (MNH). FRENCH GUIANA: Cayenne, ♀ (MCZ). COLOMBIA: *Dept. Chocó.* Quibdó, ♀ (IMLT). *Meta.* 20 km N Río Muco, "Carimagua," ♀, ♂ (MCZ); 15 km SW Puerto Lopez, ♀, ♂ (MCZ); 20 km S El Porvenir, ♀ (MCZ). Villavicencio, ♀ (AMNH). *Valle.* Cali, ♂ (MCZ); nr. Cali, 1,000 m, ♂ (MCZ); 50 km S Buenaventura, ♀ (MCZ); 28 km E Buenaventura, ♀ (MCZ). *Huila.* 10 km E Leticia, ♂ (MCZ). *Cauca.* NW Guapi, 100 m, ♀ (MCZ). *Caqueta.* Río Orteguaza, ♀ (AMNH). ECUADOR: *Prov. Pichincha.* 16 km SE San Domingo, Tinandia (?), ♂ (MCZ); 10 km W Santo Domingo de los Colorados, ♀ (CAS); km 113 vía Pto. Quito, ♀ (MECN). *Napo.* Tayos Santiago, ♀ (MCZ); Tarapuy, 2♀ (MECN). *Guayas.* Milagro, ♀, ♂ (EPC). *Los Ríos.* 50 km E Quevado, ♀ (CAS); Juan Montalvo, ♀ (AMNH). *El Oro.* Río Santa Rosa, 64 km S of Ista Rosa, ♂ (EPC). PERU: *Dept. Amazonas.* Río Alto Marañón, betw. Río Campa and Río Nieva, ♀ (AMNH). *Loreto.* Iquitos, ♀ (MCZ); Río Napo, ♀ (MCZ). *Huánuco.* 69 km E Tingo María, ♀ (CAS); Tingo María, 15♀, 3♂ (CAS, AMNH); Santa Teresa, ♀ (EPC); Cucharas, ♂ (EPC); Divisoria, ♀ (AMNH). *Pasco.* Puerto Bermúdez, ♀ (CUC). *Junín.* Estancia Naranjal San Ramon, 1,000 m, 2♀ (AMNH). BRAZIL: *Est. Amazonas.* Tefé, 2♀ (MCZ, BMNH); Alto Solimões, ♀, ♂ (FZRS); Rio Negro, Umarituba, ♀ (NRS); Rio Autas, Cururuzinho, ♀ (NRS); Lagode Coarí, ♀ (NRS). *Pará.* Belém, ♀ (MCZ); Canindé, ♀ (AMNH); Jacaré-Acanga, ♀ (AMNH); Santarém, Monte Alegro, ♀ (BMNH). *Rondônia.* Abuña, ♀, ♂ (MCZ); Pôrto Velho, ♀ (MCZ). *Mato Grosso.* 260 km N Xavantina, ♀ (MCZ); Chavantina, ♀ (MSP). *Goiás.* Corumbá, ♀ (MZSP). *Bahia.* Iguassú, ♀

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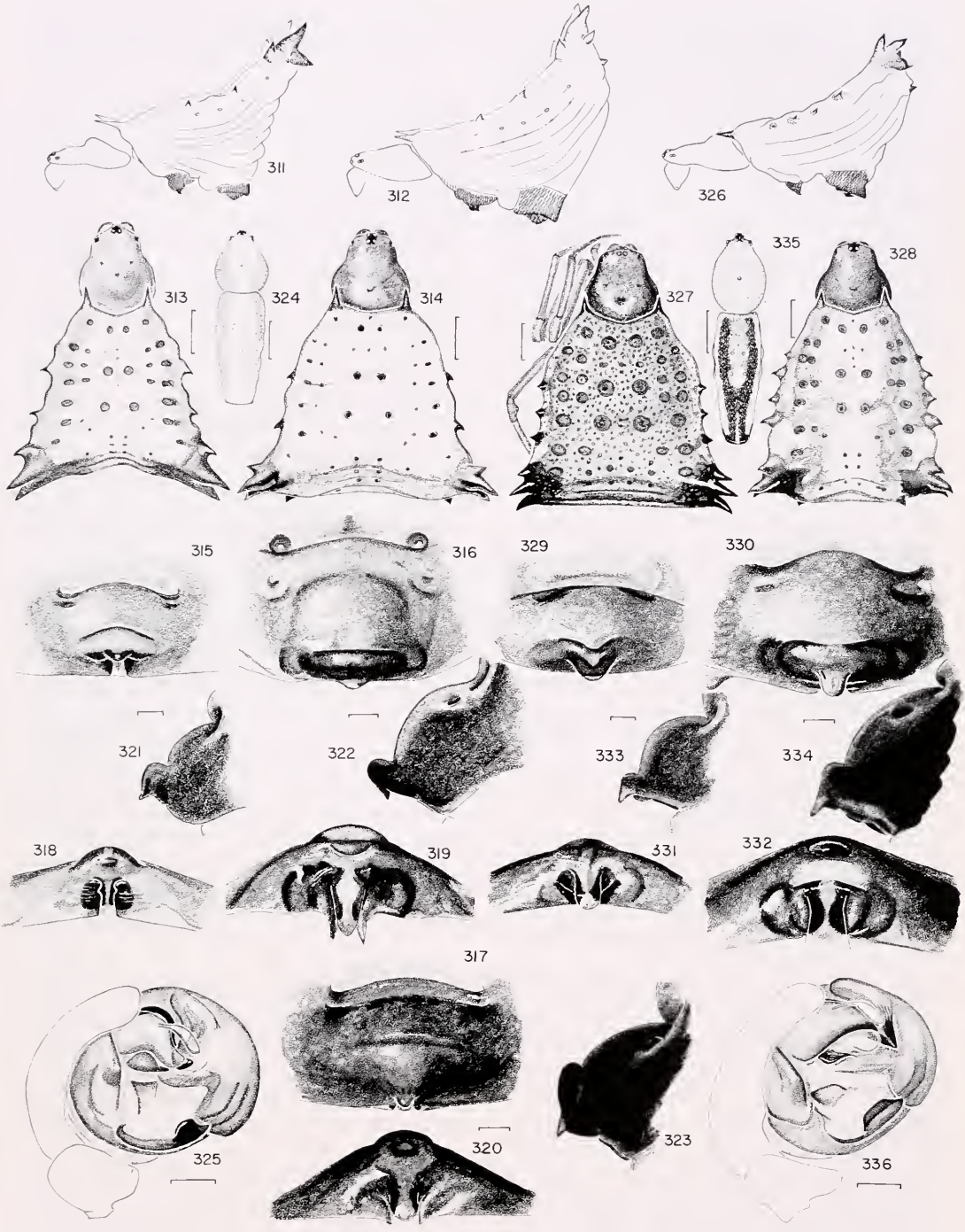
Figures 311–325. *Micrathena plana* (C. L. Koch). 311–323. Female. 311, 312. Lateral. 313, 314. Dorsal. 315–317. Epigynum, dorsal. 318–320. Epigynum, posterior. 321–323. Epigynum, lateral. 311, 313, 315, 318, 321. (Dept. Meta, Colombia). 312, 314, 317, 320, 323. (Dept. Junín, Peru). 316, 319, 322. (Est. Mato Grosso, Brazil). 324, 325. Male. 324. Dorsal. 325. Left palpus, mesal.

Figures 326–336. *Micrathena triangularis* (C. L. Koch). 326–334. Female. 326. Lateral. 327, 328. Dorsal. 329, 330. Epigynum, ventral. 331, 332. Epigynum, posterior. 333, 334. Epigynum, lateral. 326, 328, 330, 332, 334. (Suriname). 327. (Cayenne). 329, 331, 333. (Belém, Brazil). 335, 336. Male. 335. Dorsal. 336. Palpus, mesal.

Scale lines. 0.1 mm, except Figures 311–314, 324, 326-328, 335, 1.0 mm.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(NRS). *Minas Gerais.* Belo Horizonte, ♂ (CUC). *Espírito Santo.* Colatina, ♀ (MNRJ). *Rio de Janeiro.* Angra dos Reis, ♀ (MZSP). *São Paulo.* Batatais, ♀ (MZSP); Boa Esperanjo do Sul, 3♀ (MZSP); Nova Europa, 2♀, ♂ (MZSP); Cosmopolis, ♀ (CAS); Rio Claro, ♀ (FAM); Guatapará, ♂ (MZSP); Tabatinga, ♂ (MZSP); São Roque, ♀ (MZSP); Pirassununga, ♀ (MZSP). *Rio Grande do Sul.* Garruchos São Borja, ♀, ♂ (FZRS). São Francisco de Paula, 2♀ (FZRS). BOLIVIA: *Dept. Beni.* Rio Beni [66:W, 12:30S], ♀ (AMNH). *Cochabamba.* Gral. Roman, ♀ (MULP). PARAGUAY: *Dept. Concepción.* Territ. Foncière, 7♀ (MCZ, NMW); Apa, ♀ (AMNH). *Caaguazú.* Colón. Walter Instrán, 4♀ (JAK). *Alto Paraná.* Pto. Stroessner, 2♀ (MHNG); km 12 de Stroessner, ♀ (JAK). *Itapu.* Isla Yacreta, ♀ (MACN). BOLIVIA: *Dept. Beni.* Río Beni, ♀ (AMNH). *Cochobamba.* Gral. Roman, ♀ (MULP). ARGENTINA: *Prov. Misiones.* San Ignacio, 4♀ (MULP); Iguazú, 4♀ (MULP, MEG); Pindapoy, ♀ (MULP); Montecarlo, 2♀ (MEG); Punta 17 de Octubre, many ♀, 3♂ (MACN); Santa María, 2♀ (MACN); Aguarai-Guazú, ♀ (MACN); Rio Iguazú, on rd. to Iguazú, ♀ (MACN); Rio Uruguai, nr. Pto. Bemberg, ♀ (MACN).

Micrathena triangularis (C. L. Koch) Figures 326–336; Map 6

Acrosoma triangulare C. L. Koch, 1836: 78, fig. 226. Female from Brazil (ZSM), destroyed.

Acrosoma pilosa Taczanowski, 1873: 271, pl. 5, fig. 23, ♀. Two female and two juvenile syntypes from Uassa, French Guiana [Uaça, Amapá, Brazil] (PAN), examined. NEW SYNONYMY.

Acrosoma sordida Taczanowski, 1873: 273, pl. 6, fig. 25, ♀. Female holotype from Cayenne, French Guiana (PAN), examined. NEW SYNONYMY.

Acrosoma gibbosum Taczanowski, 1879: 113, pl. 1, fig. 30, ♀. Four female syntypes from Amable María [Junín], Peru (PAN), examined. NEW SYNONYMY.

Micrathena sordida:—Reimoser, 1917: 105, pl. 4, fig. 8, ♀. Roewer, 1942: 964.

Micrathena triangularis:—Reimoser, 1917: 107, pl. 5, fig. 10, ♀. Roewer, 1942: 965. Bonnet, 1957: 2880.

Micrathena pilosa:—Roewer, 1942: 961.

? *Micrathena ruschi* Mello-Leitão, 1945b: 266, figs. 7–9, ♀. Female from Santa Teresa, Est. Espírito Santo, Brazil (MNRJ), lost. DOUBTFUL NEW SYNONYMY.

Micrathena gertschi Chickering, 1964: 261, figs. 23–29, ♂. Male holotype from Simla, Trinidad, Lesser Antilles (AMNH), examined. NEW SYNONYMY.

Synonymy. C. L. Koch gave an adequate description and illustration of this species. *Acrosoma pilosa, sordida* and *gibbosum* appear to be females of this species from French Guiana and Peru; *M. gertschi* is the male.

Mello-Leitão's illustration of a female with 18 spines and elongate sternum and genital area are probably this species.

Description. Female from French Guiana. Carapace, sternum dark brown, legs brown. Dorsum of abdomen brownish black, with large and small sclerotized discs darker brown; white edge on each side and an indistinct transverse white edge on the posterior; sides with white marks; venter between epigynum and spinnerets dark brown; dark brown ring around spinnerets. Carapace with one pair of dimples; thorax very high (Fig. 326). Abdomen trapezoidal with 14 to 16 spines; many large circular discs on the dorsum and sides, and many tiny sclerotized spots in between (Fig. 327). Total length, 6.8 mm. Carapace, 2.3 mm long, 2.1 mm wide. First femur, 2.3 mm; patella and tibia, 2.3 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm. Second patella and tibia, 2.1 mm; third, 1.3 mm. Fourth femur, 2.5 mm; patella and tibia, 2.0 mm; metatarsus, 1.4 mm; tarsus, 0.6 mm.

Male holotype of *M. gertschi.* Carapace dusky brown, head dark with narrow median lighter area between thoracic mark and posterior edge. Sternum dark dusky brown. Coxae, legs yellow-white. Dorsum of abdomen with two dark paraxial bands, lighter marks in between (Fig. 335), sides and venter black. Carapace with round thoracic mark. First coxa with hook; groove on second femur. First and second legs with macrosetae. Abdomen longer than wide, narrowest posteriorly, sides slightly wavy (Fig. 335). Total length, 4.5 mm. Carapace, 1.8 mm long, 1.2 mm wide. First femur, 1.7 mm; patella and tibia, 1.6 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm. Second patella and tibia, 1.2 mm;

third, 0.8 mm. Fourth femur, 1.8 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 5.8 to 7.4 mm, males from 4.3 to 4.9 mm. Females may have an additional small pair of spines in front of the second pair (the first laterals, Fig. 328). Others from Peru have an additional pair of small spines on the posterior behind and below the seventh pair (Fig. 326). Females usually have 14 spines, but sometimes 16; rarely 18. The density of tiny sclerotized spots on the dorsum of the abdomen is variable.

Some females from southern Brazil have the characteristic epigynum but lack the middle lateral spines (as in *M. plana*); they have four spines, one posteriorly on each side. Some few specimens from Colombia, Peru, and Brazil have the characteristic spines, but have the transverse bar swollen as in *M. plana*. Do the two species hybridize?

Note. A male was collected with a female in Suriname by Debby Smith, and males are in collections with females from Cucharas, Peru.

Diagnosis. Females can be distinguished from *M. duodecimspinosa* and *M. plana* by the additional pair of spines on the sides of the abdomen (Figs. 327, 328). They differ from *M. plana* and *M. quadriserrata* by the concave or straight anterior margin of the transverse bar of the epigynum, and by its wide median lobe (Figs. 329, 330). They differ from *M. excavata* by lacking the ventral spines or tubercles above the spinnerets (Fig. 326). Usually females have the abdomen more sclerotized than that of *M. plana*.

The male differs from that of related species by the pointed terminal apophysis and by the sclerotized pointed conductor (Fig. 336).

Natural History. Specimens have been taken from gallery forest in Mato Grosso.

Distribution. Trinidad, northern South America to Peru and southern Brazil (Map 6).

Records. LESSER ANTILLES: *Trinidad.* common, ♀, ♂ (AMNH, MCZ). VENEZUELA: *Est. Carabobo.* San Esteban, ♀ (CUC). *Aragua.* Rancho Grande, ♀ (AMNH). *Monagas.* Caripito, ♀ (AMNH). *Bolívar.* Hato la Vergarena, ♀ (AMNH). GUYANA: nr. Mazaruni, Pakaraima Mts., ♀ (CUC); Ireng Riv., Roraima, ♀ (AMNH). Upper Essequibo Riv., ♀ (AMNH). Canje, Ikurua Riv., ♀ (AMNH). Kaieteur, ♀ (AMNH). Kartabo, ♀ (AMNH). SURINAME: upper Surinam Riv., ♀ (BMNH). *Saramacca Prov.* Voltzberg-Raleighvallen Nature Reserve, ♀, ♂ (MCZ). *Brokopondo.* Browns Berg, ♀ (MCZ). FRENCH GUIANA: Cayenne, ♀, 4♂ (PAN). COLOMBIA: *Dept. Antioquia.* Mutatá Cancheras, ♀ (MCZ). *Santander.* Río Suárez, ♀ (AMNH). *Cundinamarca.* Bogotá, ♀ (BMNH). Río Suárez, ♀ (AMNH). *Meta.* Villavicencio, ♀ (CAS), ♀ (MCZ); 45 km N Villavicencio, 1,500 m, 2♀ (AMNH, CAS). PERU: *Dept. Loreto.* La Frontera, Upper Utoquinia, ♀ (AMNH); Río Igara, Parandi tributary of Putumayo, ♀ (BMNH). *San Martín.* 20 km NE Moyobamba, 1,600 m, 3♀ (AMNH). *Huánuco.* Cucharas, ♀, ♂ (F. Woytkowski, EPC); Tingo María, 9♀, ♂ (AMNH, CAS); near Ucayacu, 2♀ (AMNH). BRAZIL: *Est. Pará.* Canindé, 7♀ (AMNH); 50 km E Canindé, 7♀ (AMNH); Cachoeira, ♀ (IBSP); Rio Gurupi, 2♀, ♂ (MSP); Santarém, 11♀ (BMNH); Belém, 7♀ (AMNH, MACN, MCZ, MEG); km 305 Ligaçao-Belém, ♀ (MZSP); Jacaréacanga, ♀ (AMNH). *Amazonas.* Rio Autás, Cururú, ♂ (NRS); Rio Autás, Cururuzinho, 6♀ (NRS); Manaus, 7♀ (INPA, MEG, NRS); Rio Negro, Umarituba, ♀ (NRS). *Amapá.* Villa Amazonas, 4♀ (CAS); Serra do Navío, ♀ (CAS). *Rondônia.* Pôrto Velho, 2♀ (AMNH, MCZ). *Mato Grosso.* Chapada dos Guimaroes, 2♀ (AMNH); 260 km N Xavantina (MCZ). *Bahia.* Iguassú, ♀ (NRS); Salvador, ♀ (SMK). *Espírito Santo.* Goitacazes, ♀ (MNRJ); Rio São José, 5♀ (MZSP). *Rio de Janeiro,* Petrópolis, 4♀ (MNRJ). *São Paulo.* Nova Europa, ♀ (MZSP); Boracéia, 2♀ (MZSP); Campos de Serra, ♀ (MZSP); Salesópolis, ♀ (MZSP). *Paraná.* Curitiba, 2♀ (MNRJ); Paranagua, ♀ (MNRJ). *Santa Catarina.* Blumenau, 2♀

(MZSP), 3♀ (BMNH), 6♀ (NMW); Joinville, 4♀ (MNRJ). *Rio Grande do Sul.* Vila Oliva, ♀, ♂ (FZRS). BOLIVIA: *Dept. Cochabamba.* Gral. Roman, 5♀, 2♂ (MULP); Chapare, ♀ (MULP). PARAGUAY: *Dept. Alto Paraná.* Taguaranapa, 3♀ (EPC). *Concepción.* Territ. Foncière, 2♀ (MCZ); [? Río] Apa (AMNH). ARGENTINA: *Prov. Salta.* El Tabacal, 2♀ (MACN); Cartagal, 5♀ (MACN); Santa María, 4♀ (MACN).

Micrathena huanuco new species
Figures 337–341; Map 6

Holotype. Female with three paratypes (1 MCZ, 2 EPC) from Cucharas, Huallaga Valley, Dept. Huánuco, Peru, Feb.–April 1954 (F. Woytkowski, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange-brown. Sternum, legs dark brown. Dorsum of abdomen orange-brown with tiny white pigment spots posteriorly and on each side; venter with black streaks on brown. Carapace with thoracic depression and high thorax; no dimples, no rim in dorsal view. Eyes subequal in size. Abdomen subtriangular with a pair of spines overhanging carapace, a large posterolateral double spine, and four pairs of small lateral spines (Figs. 337, 338). Total length, 6.0 mm. Carapace, 2.4 mm long, 2.0 mm wide. First femur, 2.4 mm; patella and tibia, 2.4 mm; metatarsus, 1.4 mm; tarsus, 0.6 mm. Second patella and tibia, 2.2 mm; third, 1.4 mm. Fourth femur, 2.6 mm; patella and tibia, 2.2 mm; metatarsus, 1.6 mm; tarsus, 0.6 mm.

Variation. Females vary in total length from 6.0 to 7.2 mm.

Diagnosis. This species differs from *M. parallela* in the posterior view of the epigynum (Fig. 340) and having four pairs of spines on the side and none below the posterolateral double spine (Figs. 337, 338). It differs from the sympatric *M. exlinae* by being larger, having the median piece of the epigynum with almost parallel sides (Fig. 340), and by having black pigment on the sternum and black streaks on the venter of the abdomen from the spinnerets to the posterolateral double spine and up the sides. It differs from *M. plana* and *M. triangularis* by having only two posterodorsal spines (Fig. 337).

Micrathena exlinae new species
Figures 342–346; Map 6

Holotype. Female with one paratype from Cucharas, Huallaga Valley, Huánuco, Peru, Feb.–April 1954 (F. Woytkowski, MCZ). The species is named after the late Harriet Exline, who started a revision of *Micrathena* of western South America.

Description. Female. Carapace orange, head lightest, sides of thorax dark. Sternum orange, coxae lighter orange; distal articles of legs dusky orange. Dorsum of abdomen orange, large spines underlain by some white pigment spots; sides dusky orange; venter light orange, sclerotized areas darker. Carapace with high thorax and thoracic depression; lacking dimples. Posterior median eyes 1.3 diameters of anterior medians; laterals 0.8 diameters. Total length, 5.6 mm. Carapace, 1.9 mm long, 1.7 mm wide. First femur, 2.2 mm; patella and tibia. 2.2 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm. Second patella and tibia, 1.8 mm; third, 1.0 mm. Fourth femur, 2.3 mm; patella and tibia, 1.9 mm; metatarsus, 1.4 mm; tarsus, 0.6 mm.

Diagnosis. This species differs from *M. huanuco* by having a bottle-shaped septum on the posterior face of the epigynum

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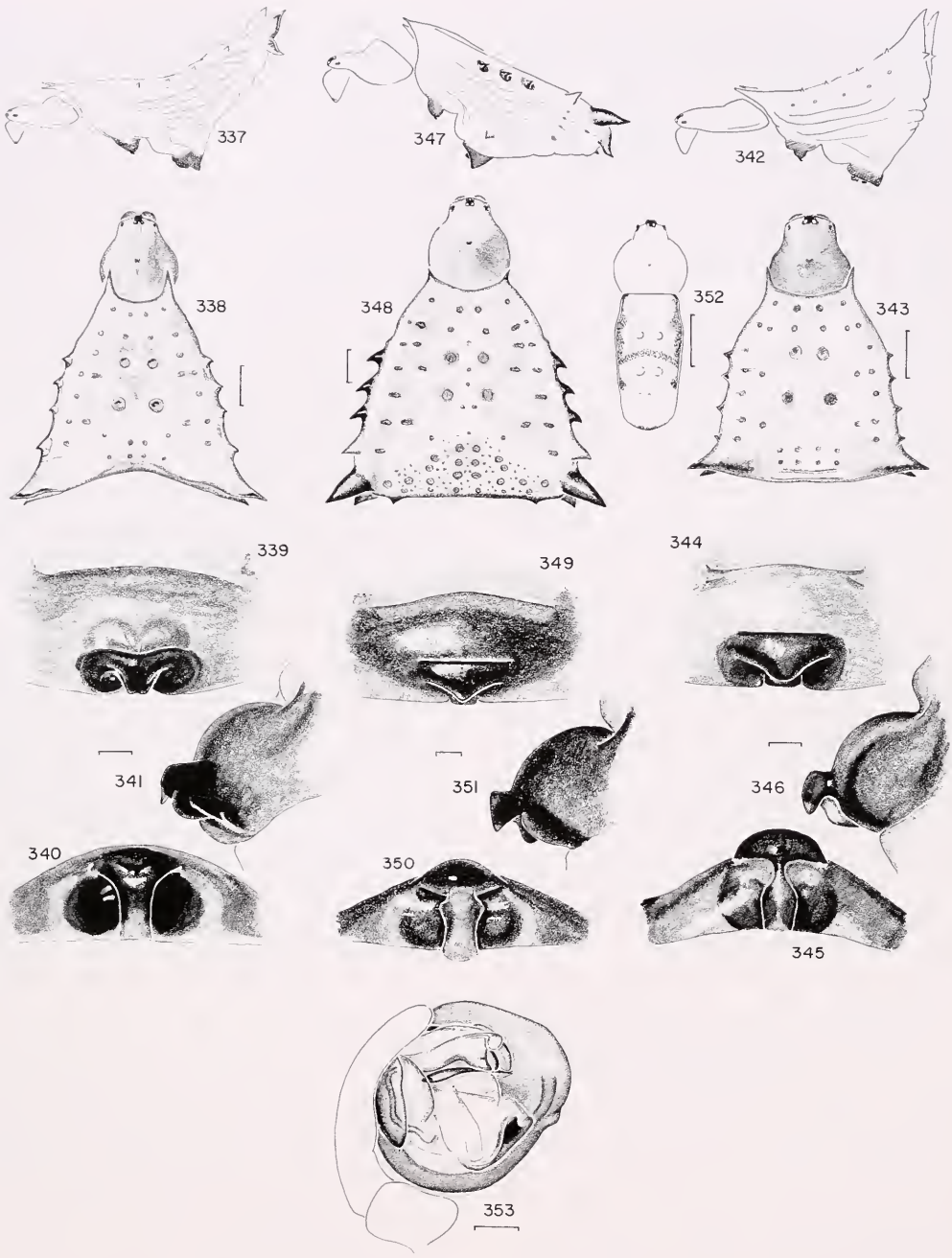
Figures 337–341. *Micrathena huanuco* n. sp., female. 337. Lateral. 338. Dorsal. 339. Epigynum, ventral. 340. Epigynum, posterior. 341. Epigynum, lateral.

Figures 342–346. *Micrathena exlinae* n. sp., female. 342. Lateral. 343. Dorsal. 344. Epigynum, ventral. 345. Epigynum, posterior. 346. Epigynum, lateral.



Figures 347–353. *Micrathena excavata* (C. L. Koch). 347–351. Female. 348. Dorsal. 349. Epigynum, ventral. 350. Epigynum, posterior. 351. Epigynum, lateral. 352, 353. Male. 352. Dorsal. 353. Left palpus, mesal.

Scale lines. 0.1 mm, except Figures 337, 338, 342, 343, 347, 348, 352, 1.0 mm.

(Fig. 345). It differs from *M. triangularis* by having only two posterodorsal spines (Figs. 342, 343).

Paratypes. PERU: *Dept. Huánuco.* Cucharas, ♀ (AMNH); Santa Teresa, Río Huallaga, 6,000 m el., Aug. 1954, ♀ (F. Woytkowski, EPC).

Micrathena excavata (C. L. Koch)
Figures 347–353; Map 6

Acrosoma excavatum C. L. Koch, 1836: 80, pl. 227, ♀. Female holotype from Brazil (ZSM), destroyed.
Micrathena excavata:—Reimoser, 1917: 108, pl. 5, fig. 9, ♀. Roewer, 1942: 957. Bonnet, 1957: 2866.
? *Micrathena mirifica* Chickering, 1961: 437, figs. 117–121, ♂. Male holotype from Barro Colorado Island, Panama (MCZ), examined. DOUBTFUL SYNONYMY.
Micrathena subflava Chickering, 1961: 461, figs. 189–193, ♀. Female holotype from Barro Colorado Island, Panama Canal Zone (MCZ), examined. NEW SYNONYMY.

Synonymy. C. L. Koch described the diagnostic light colored fourth lateral pair of spines situated between darker spines. Chickering did not know of Koch's species and described it as a new species, *M. subflava. Micrathena mirifica* is perhaps the male of this species.

Description. Female from French Guiana. Carapace, sternum, legs orange. Sternum with indistinct posterior gray patch. Dorsum of abdomen light orange; anterior three pairs of lateral spines and large posterolateral spine black, spine in between light (Fig. 348); sides, venter light orange. Epigynum and ring around spinnerets black. Carapace without dimples or rim, thorax high (Figs. 347, 348). Total length, 7.5 mm. Carapace, 2.5 mm long, 2.3 mm wide. First femur, 2.7 mm; patella and tibia, 2.7 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm. Second patella and tibia, 2.3 mm; third, 1.4 mm. Fourth femur, 2.9 mm; patella and tibia, 2.4 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm.

Male. Carapace orange, sternum light orange with gray mark posteriorly. Dorsum of abdomen white with black marks (Fig. 352); venter yellow-white with a black mark behind spinnerets. Carapace smooth with a median thoracic mark. First coxa without hook. First and second legs with macrosetae. Total length, 4.1 mm. Carapace, 1.8 mm long, 1.6 mm wide. First femur, 1.7 mm; patella and tibia, 1.7 mm; metatarsus, 1.2 mm; tarsus, 0.5 mm. Second patella and tibia, 1.4 mm; third, 0.8 mm. Fouth femur, 1.6 mm; patella and tibia, 1.2 mm; metatarsus, 1.0 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 7.3 to 9.2 mm. Compared to related species there is little variation, and all specimens appear alike. The first three pairs of lateral spines may be light in color, the fourth always is.

Note. M. mirifica may be the male of this species, although it lacks a coxal hook (characteristic of this species group) and has not been collected with a female. The male has a uniformly colored carapace, and a gray spot on the light sternum, as do females.

Diagnosis. Females differ from related species by their slightly larger size, by having 18 pairs of spines, and by the light colored fourth lateral pair of spines in front of the black posterolaterals. They also have an unusual pair of soft, light colored ventral spines (or tubercles), one on each side of the spinnerets (Fig. 347).

Males differ from others of this species group by lacking the coxal hook, by the thorn-shaped rim of the median apophysis, and by the shape of the terminal apophysis (Fig. 353).

Distribution. From Panama to Peru and Brazil (Map 6).

Records. PANAMA: *Prov. Panamá,* Canal Area. Barro Colorado Island, many collections, ♀, ♂ (AMNH, MCZ); Pipeline Rd., ♀ (MCZ); Fort Sherman, ♀ (UPMI). VENEZUELA: *Est. Bolívar.* Mato la Vergarena [6:45N, 63:30W], 25 Oct. 1954, ♀ (AMNH). GUYANA: Kartabo, 1924, ♀ (CUC). PERU: *Dept. Huánuco.* Tingo María, 670 m, ♀ (AMNH, EPC). BRAZIL: *Terr. Amapá.* Uaçá, ♀ (PAN). *Est. Pará.* Canindé, 1964, ♀ (J. Carvalho, AMNH). *São Paulo.* Ubatuba, ♀ (MZSP); Pôrto

Cobral, ♀ (MZSP). *Paraná.* Paragua, ♀ (MNRJ). *Santa Catarina.* ♀ (NMW). ARGENTINA: *Prov. Misiones.* Parque Nac. Iguazú, ♀ (MEG); Santa María, 2♀ (MACN); Pto. Bamberg, ♀ (MACN).

Micrathena marta new species
Figures 354–358; Map 6

Holotype. Female from Río Frío, 30 km E of Santa Marta, Dept. Magdalena, Colombia, 2 July 1927 (G. Salt, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, sternum, coxae orange. Legs black. Abdomen black except for a ventral pair of white spots on each side, slightly anterior of spinnerets. Carapace with high thorax, one pair of dimples, and thoracic depression. Posterior median eyes slightly larger than others, which are subequal. Abdomen with 16 spines (Figs. 354, 355). Total length, 5.6 mm. Carapace, 2.0 mm long, 1.6 mm wide. First femur, 1.6 mm; patella and tibia, 1.7 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm. Second patella and tibia, 1.5 mm; third, 0.9 mm. Fourth femur, 1.9 mm; patella and tibia, 1.4 mm; metatarsus, 1.1 mm; tarsus, 0.5 mm.

Variation. The third pair of spines, the second on the sides, is almost lacking on the right side but not on the left (Fig. 355).

Diagnosis. This species differs from *M. bananal* by being larger, having a yellow sternum, and by the more flattened shape of the epigynum (Fig. 356).

Micrathena bananal new species
Figures 359–363; Map 6

Holotype. Female from Santa Isabel do Moro [12°S, 51°W], Ilha do Bananal, Est. Goiás, Brazil, June 1981 (M. Alvarenga, AMNH). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace brown, darker on sides. Sternum blackish brown. Coxae and distal articles of legs orange, darkest distally. Dorsum of abdomen white, dusky on sides; sides black; venter black with a white longitudinal band on each side and white patches behind spinnerets. Carapace with thoracic depression and one pair of dimples; thorax very high. Posterior median eyes slightly larger than others, which are subequal in size. Abdomen shield-shaped with fourteen spines: the large first pair overhangs the carapace; three tiny pairs on sides, and three larger posterolaterals (Figs. 359, 360). Total length, 5.0 mm. Carapace, 1.9 mm long, 1.5 mm wide. First femur, 1.7 mm; patella and tibia, 1.8 mm; metatarsus, 1.0 mm; tarsus, 0.5 mm. Second patella and tibia, 1.5 mm; third, 1.0 mm. Fourth femur, 2.1 mm; patella and tibia, 1.6 mm; metatarsus, 1.2 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 4.8 to 5.0 mm.

Diagnosis. This species differs from the sympatric *M. alvarengai* by having only 14 spines on the abdomen (Figs. 359, 360) and a wider lobe of the epigynum (Fig. 361). It differs from *M. plana* by having the anterior margin of the transverse bar of the epigynum straight (Fig. 361); from *M. huanuco* and *M. exlinae* by having three pairs of posterolateral spines (Fig. 359); and from *M. triangularis* by the parallel sides of the abdomen (Fig. 360) and the different profile of the epigynum (Fig. 363). It differs from the similar *M. marta* by being smaller and by having a black sternum.

Paratype. BRAZIL: *Prov. Bahia.* Iguassú, Rio Una, 3 July 1924, ♀ (A. Roman, NRS).

Micrathena alvarengai new species
Figures 364–368; Map 6

Holotype. Female holotype from Santa Isabel de Moro [12°S: 51°W], Ilha do Bananal, Est. Goiás, Brazil, June 1961 (M. Alvarenga, AMNH). The species is named after the collector.

Description. Female. Carapace dark orange-brown, sides blackish. Sternum blackish brown. Coxae orange, distal leg articles orange-brown. Dorsum of abdomen white, with dusky area on each side and a black patch on each side on posterolateral spines; sides black; venter black,

with indistinct white band on each side. Carapace with one pair of very distinct dimples anteriorly and distinct thoracic depression; thorax unusually high, with depression on anterior of thoracic slope. Posterior median eyes slightly larger than anterior medians; laterals subequal to anterior median eyes. Abdomen squarish with a pair of large spines overhanging carapace, and eight equally spaced pairs of spines (Fig. 365). Total length, 5.0 mm; Carapace, 1.8 mm long, 1.4 mm wide. First femur, 1.6 mm; patella and tibia, 1.7 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm. Second patella and tibia, 1.4 mm; third, 0.9 mm. Fourth femur, 1.9 mm; patella and tibia, 1.6 mm; metatarsus, 1.2 mm; tarsus, 0.5 mm.

Diagnosis. This species differs from *M. bananal* by having 18 spines on the abdomen (Figs. 364, 365). It differs from *M. triangularis* by the shape of the epigynum in profile, and by having a light spot behind the lobe of the epigynum (Figs. 367, 368).

Micrathena quadriserrata F. P.-Cambridge
Figures 369–375; Map 6

Micrathena uncata F. P.-Cambridge, 1904: 533, pl. 50, fig. 14, ♂. Male holotype from Guatemala (BMNH), examined. Roewer, 1942: 965. Bonnet, 1957: 2881. Chickering, 1962: 466, figs. 202–205, ♂. NEW SYNONYMY.

Micrathena quadriserrata F. P.-Cambridge, 1904: 534, pl. 50, fig. 18, ♀. Four juvenile syntypes from Quezaltepeque, Guatemala (BMNH) examined. Reimoser, 1917: 94, pl. 3, fig. 4, ♀. Roewer, 1942: 962. Bonnet, 1957: 2875. Chickering, 1961: 448, figs. 146–149, ♀.

Chaetacis rouxi Mello-Leitão, 1939: 68, figs. 45–47, ♀. Female holotype from Prov. Falcón, Venezuela (NMB), examined. NEW SYNONYMY.

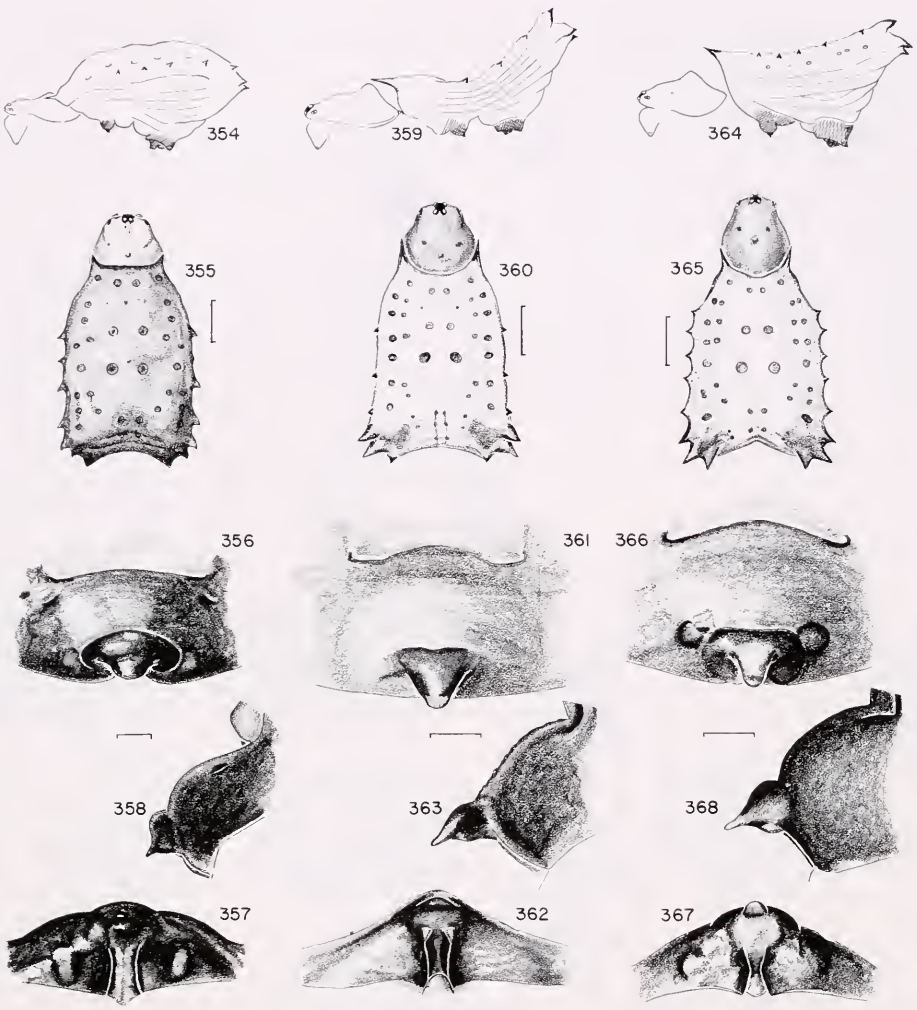
Micrathena modica Chickering, 1961: 439, figs. 122–126, ♂. Male holotype from Summit, Panama (MCZ), examined. NEW SYNONYMY.

Synonymy. Micrathena uncata is the male of *M. quadriserrata*. Although the name *uncata* has page priority, it is preferable to use that of the female *M. quadriserrata*. The type of *M. uncata* is in poor condition; details had to be illustrated (and reversed) from the right palpus (Fig. 375). The type of *C. rouxi* Mello-Leitão does not differ from other specimens of this species. Chickering (1962) did not notice the similarity of the palpi of *M. uncata* and his new *M. modica*, since he characteristically drew each from a different angle. He noted that both lacked coxal hooks. The type of *M. uncata* has a hook, however.

Description. Female from Panama. Carapace light orange, sides blackish orange. Sternum with black pigment. Coxae orange; distal leg articles blackish on orange. Dorsum of abdomen white with dark patches (Fig. 370); venter black with a pair of paraxial white bands, one on each side. Carapace with one anterior pair of dimples, a median thoracic mark, and a very high thorax. Abdomen with two sharp anterior spines, two pairs of denticles on the sides, and a posterior lobe on each side with three or four teeth (Figs. 369, 370). Total length, 6.0 mm. Carapace, 2.3 mm long, 1.9 mm wide. First femur, 2.4 mm; patella and tibia, 2.6 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm. Second patella and tibia, 2.2 mm; third, 1.3 mm. Fourth femur, 2.7 mm; patella and tibia, 2.1 mm; metatarsus, 2.0 mm; tarsus, 0.5 mm.

Male. Carapace orange-brown. Sternum, legs brown. Dorsum of abdomen grayish white with dark patches; venter black. Carapace with median thoracic depression; no dimples (Fig. 374). First coxa with small posterior hook, second femur with groove. Total length, 5.8 mm. Carapace, 2.1 mm long, 1.7 mm wide. First femur, 2.2 mm; patella and tibia, 2.0 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm. Second patella and tibia, 1.9 mm; third, 1.0 mm. Fourth femur, 2.3 mm; patella and tibia, 1.7 mm; metatarsus, 1.4 mm; tarsus, 0.6 mm.

Variation. Females vary in total length from 5.2 to 7.4 mm, males from 4.5 to 5.8 mm. Some females have the dorsum of the abdomen all black. The posterolateral lobes of the abdomen may be much longer than those in Figure 370, and may sometimes be twisted into a vertical posi-



Figures 354–358. *Micrathena marta* n. sp., female. 354. Lateral. 355. Dorsal. 356. Epigynum, ventral. 357. Epigynum, posterior. 358. Epigynum, lateral.

Figures 359–363. *Micrathena bananal* n. sp., female. 359. Lateral. 360. Dorsal. 361. Epigynum, ventral. 362. Epigynum, posterior. 363. Epigynum, lateral.

Figures 364–368. *Micrathena alvarengai* n. sp., female. 364. Lateral. 365. Dorsal. 366. Epigynum, ventral. 367. Epigynum, posterior. 368. Epigynum, lateral.

Scale lines. 0.1 mm, except Figures 354, 355, 359, 360, 364, 365, 1.0 mm.

tion. All penultimates and small adults have four spines on these lobes; larger females have the last pair of spines very small or absent. The lack of the characteristic coxal hook in males from Panama is puzzling.

Note. Females and males have been collected together in Nicaragua, Costa Rica and Panama.

Diagnosis. Females can be separated from other 12- or 14-spined species by the two posterolateral lobes of the abdomen

(Fig. 370) separated by a wide notch, and by the V-shaped transverse bar of the epigynum, often narrower in the center than on the sides. There is only a slight median lobe or none with a bulge underneath (dorsal) to it (Figs. 371–373). Females are similar to those of *M. brevispina,* which is smaller, has about 16 spines, and a deeper notch between the posterior lobes of the abdomen.

Males can be separated from others by the curved conductor and terminal apophysis, enclosing the embolus but open toward the mesal side of the palpus (Fig. 375).

Distribution. Chiapas, Mexico to Venezuela (Map 6).

Records. MEXICO: *Est. Chiapas.* Huixtla, ♀ (AMNH); Cacahuatan, ♀ (AMNH); nr. Huehuetan, ♀ (AMNH); 32 km NW Ocozocoautla, ♀ (CAS); 18 km N Tuxtla Gutiérrez, ♀ (CAS); El Sumidero, 2♀ (CAS); Montozintla, 1,000 m, ♂ (CNC); NE Los Amates, 2♀, ♂ (RL); Chiapa de Corzo, 4♀ (BC). HONDURAS: Copán, ♀ (AMNH). EL SALVADOR: San Salvador, 2♀ (AMNH); Santa Tecla, 7♀ (AMNH). NICARAGUA: nr. Managua, 10♀, ♂, 2 imm. (AMNH). COSTA RICA: *Prov. San José.* San José, 3♀, 4♂, 3 imm. (AMNH); Villa Colón, 6♀, 2♂ (MZCR); La Caja, 5♂ (NMW). *Guanacaste.* Cañas, ♀, ♂ (MZCR); Tilarán, ♀ (NMW); Bebedero, 4♀ (NMW). *Heredia.* W of Alajuela, ♀ (SRC). *Puntarenas.* nr. Esparta, 800 m, ♂ (MCZ); nr. Cabuya, ♀ (AMNH). PANAMA: *Prov. Panamá,* canal area. Miraflores Locks, ♀ (MCZ); Ft. Sherman, ♀ (MCZ); Barro Colorado Isl., many coll. (MCZ); Cocoli, 3♀ (AMNH); Summit, ♂ (AMNH); Cerro Ancón, ♀ (UPMI). VENEZUELA: *Distr. Federal.* Caracas, 6♀ (MCZ, NMW).

Micrathena triserrata F. P.-Cambridge
Plate 2; Figures 376–385; Map 6

Micrathena triserrata F. P.-Cambridge, 1904: 534, pl. 50, fig. 17, ♀. Three female syntypes from Guatemala (BMNH), examined. Reimoser, 1917: 95. Roewer, 1942: 965. Bonnet, 1957: 2881. Chickering, 1961: 464, figs. 198–201, ♀.

Types. Chickering refers to a lectotype which had an extra spine on the right side at the base of the trifid posterior lateral spine. Only three specimens, syntypes, were examined from the British Museum. Two of the three specimens had this unilateral spine, the third lacked it. One of the three specimens had the tip of the epigynum missing (Figs. 379, 382).

Description. Female syntype. Carapace, sternum dark brown, sides black. Legs dark brown, first femora black. Dorsum of abdomen blackish brown with median light patch, a pair of light patches, and some white along margin; sides dorsally whitish, venter gray-brown, sclerotized areas brown. Carapace with three pairs of dimples, a median thoracic depression, and thorax high. Abdomen with small discs, sclerotized spots dorsally (Figs. 376, 377); and 14 to 16 spines: three pairs of blunt spines on each side, and a trifid posterolateral wing whose base may have another denticle. Total length, 7.7 mm. Carapace, 2.8 mm long, 2.2 mm wide. First femur, 2.6 mm; patella and tibia, 2.7 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm. Second patella and tibia, 2.3 mm; third, 1.4 mm. Fourth femur, 3.2 mm; patella and tibia, 2.4 mm; metatarsus, 1.9 mm; tarsus, 0.7 mm.

Male. Carapace orange, sides gray. Sternum and coxae light orange; legs grayish brown. Dorsum of abdomen or-

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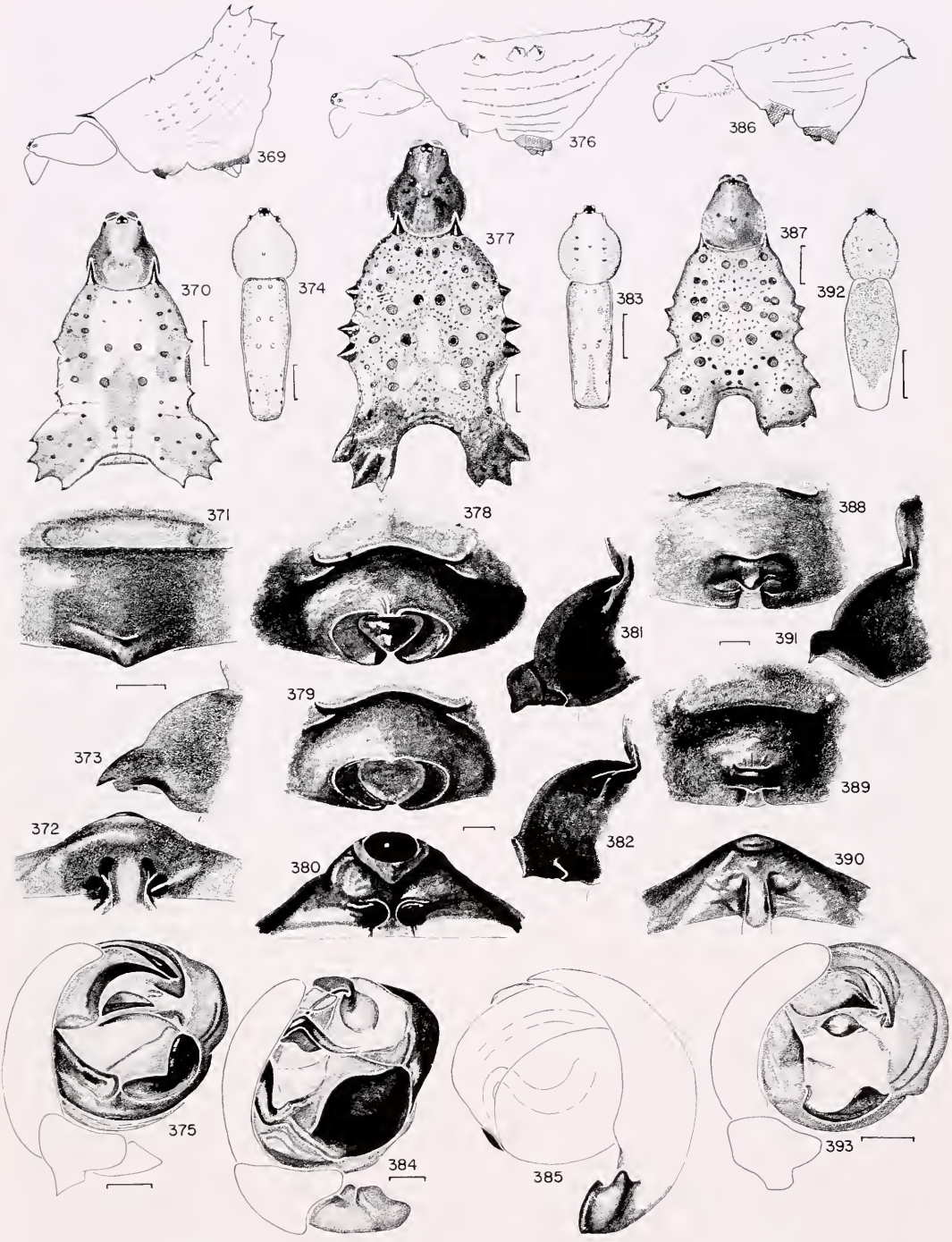
Figures 369–375. *Micrathena quadriserrata* F. P.-Cambridge. 369–373. Female. 369. Lateral. 370. Dorsal. 371. Epigynum, ventral. 372. Epigynum, posterior. 373. Epigynum, lateral. 374. 375. Male. 374. Dorsal. 375. Left palpus, mesal.

Figures 376–385. *Micrathena triserrata* F. P.-Cambridge. 376–382. Female. 376. Lateral. 377. Dorsal. 378, 379. Epigynum, ventral. 379. Lobe torn off. 380. Epigynum, posterior. 381, 382. Epigynum, lateral. 382. Lobe torn off. 383–385. Male. 383. Dorsal. 384. Palpus, mesal. 385. Palpus, lateral.

Figures 386–393. *Micrathena brevispina* (Keyserling). 386–391. Female. 386. Lateral. 387. Dorsal. 388, 389. Epigynum, ven-



tral. 390. Epigynum, posterior. 391. Epigynum, lateral. 388, 390, 391. (Argentina). 389. (Colombia). 392, 393. Male. 392. Dorsal. 393. Palpus, mesal.

Scale lines. 0.1 mm, except Figures 369, 370, 374, 376, 377, 383, 386, 387, 392, 1.0 mm.

ange-white with gray marks; venter gray and orange. Carapace with three pairs of indistinct dimples and a circular median thoracic depression (Fig. 383). First coxa with small hook, second femur with a groove. First tibia with macrosetae; second tibia with one row of five short, strong macrosetae. Total length, 4.7 mm. Carapace, 1.8 mm long, 1.4 mm wide. First femur, 1.9 mm; patella and tibia, 1.9 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm. Second patella and tibia, 1.4 mm; third, 0.8 mm. Fourth femur, 2.0 mm; patella and tibia, 1.4 mm; metatarsus, 1.2 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 7.0 to 7.7 mm. This species may have a denticle outside at the base of the trifid posterolateral lobe, sometimes only on one side (Fig. 377). The epigynum in ventral view is variable and frequently has the tip torn off (Figs. 378–382).

Note. Male and females have been collected together by W. Maddison in Campeche, Mexico.

Diagnosis. Females of this species can be distinguished from those of *M. quadriserrata* by having a median lobe on the epigynum which may be torn off (Figs. 378–382); *M. quadriserrata* lacks such a distinct lobe. The male can be differentiated from others of the species group by the large sclerotized rim of the median apophysis, the small terminal apophysis and the upside-down V-shaped paramedian apophysis (Fig. 384).

Distribution. San Luis Potosí to Belize (Map 6).

Records. MEXICO: *Est. San Luis Potosí.* 6 km W El Naranjo, 13 Dec. 1965, ♀ (G. Ball, RL). *Veracruz.* 16 km S San José del Carmen, 16 April 1953, ♀ (L. I. Davis, AMNH). Tecolutla, 13 Oct. 1947, ♂ (H. Wagner, AMNH). *Oaxaca.* 8 km E of Temascalapa, June–Aug. 1964, imm. (D. Janzen, AMNH). *Campeche.* Chicanna ruins, 8 km W of Xpujil, 12–14 July 1983, 2♀, 4♂ (W. Maddison, MCZ); 6 km W Francisco Escarcega, 11–12 July 1983, imm. (W. Maddison, MCZ). *Yucatan.* Colonia Yucatan, Aug. 1952, imm. (J. and D. Pallister, AMNH); Chichen Itza, 10 July 1948, ♀ (C. and M. Goodnight, AMNH), March 1945, ♀ (H. Wagner, AMNH). *Quintana Roo.* Kohunlich ruins, 9 km S Francisco Villa, 14–17 July 1983, ♀ (W. Maddison, R. S. Anderson, MCZ); 31 km NE Felipe Carillo Puerto, Hwy. 307, 2♀ (W. Maddison, R. S. Anderson, MCZ). *Chiapas.* Palenque ruins area, 31 July 1983, ♂ (W. Maddison, MCZ). BELIZE: El Cayo, Sept. 1959, ♀ (N. L. H. Krauss, AMNH).

Micrathena brevispina (Keyserling)
Figures 386–393; Map 6

Acrosoma brevispinum Keyserling, 1863: 70, pl. 2, fig. 3, ♀. Female type from Santa Fé de Bogota, N. Granada [Bogotá, Colombia] (BMNH), examined. Keyserling, 1892: 25, pl. 1, fig. 22, ♀.

? *Acrosoma bifissum* Keyserling, 1892: 30, pl. 1, fig. 27, imm. Female type from Blumenau [Est. Santa Catarina], Brazil, lost. DOUBTFUL SYNONYMY.

Acrosoma rubrospinosum Keyserling, 1892: 30, pl. 2, fig. 28, imm. Two juvenile syntypes from Blumenau [Est. Santa Catarina], Brazil (mislabeled as type of *bifissum*) (BMNH), examined. NEW SYNONYMY.

Micrathena brevispina:—Reimoser, 1917: 91. Roewer, 1942: 955. Bonnet, 1957: 2863. Chickering, 1960c: 68, figs. 12–14, ♀.

Micrathena mansueta Chickering, 1960c: 83, figs. 66–70, ♂. Male holotype from the Amazon (HEO), examined. NEW SYNONYMY.

Synonymy. The types of *rubrospinosum* are labeled *bifissum.* But both *A. bifissum* and *A. rubrospinosum* are probably this species. Chickering named the male *M. mansueta.*

Description. Female from Colombia. Carapace, legs brown, sternum dark brown. Dorsum of abdomen whitish; venter of abdomen black. Carapace with a pair of shallow dimples in groove between head and thorax, and circular thoracic depression; thorax hairy on sides. Abdomen dorsally flattened (Figs. 386, 387). Total length, 5.4 mm. Carapace, 1.8 mm long, 1.6 mm wide. First femur, 1.8 mm; patella and tibia, 1.8 mm; metatarsus, 1.0 mm; tarsus, 0.5 mm. Second patella and tibia, 1.7 mm; third, 1.0 mm. Fourth fe-

mur, 2.0 mm; patella and tibia, 1.7 mm; metatarsus, 1.2 mm; tarsus, 0.5 mm.

Male from Colombia. Carapace, sternum dark brown. Coxae and remaining leg articles yellowish with some gray pigment on anterior of first pair of legs. Dorsum of abdomen with a black patch, white pigment all around; venter with a median wide black band, narrower behind than anteriorly, continuing beyond spinnerets to posterior tip. Carapace with distinct median depression, pair of very slight anterolateral dents, and many hairs (Fig. 392). First coxa with hook, second femur with groove. First two legs with macrosetae. Abdomen much longer than wide, slightly lobed anteriorly (Fig. 392), and narrower behind than in front. Total length, 4.2 mm. Carapace, 1.6 mm long, 1.2 mm wide. First femur, 1.4 mm; patella and tibia, 1.3 mm; metatarsus, 0.7 mm; tarsus, 0.3 mm. Second patella and tibia, 1.0 mm; third, 0.6 mm. Fourth femur, 1.5 mm; patella and tibia, 1.0 mm; metatarsus, 0.7 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 4.5 to 6.2 mm. Many have an entirely black abdomen; others have only black patches, or the abdomen may be white. The specimen from Chiriquí, Panama has only two spines on each side, and may belong to a different species.

Note. A male has been collected with females by W. Eberhard at Río Jamundi, Dept. Valle, Colombia.

Diagnosis. The female differs from related species by the shape of the abdomen (Fig. 387) and the short transverse bar of the epigynum (Figs. 388–390). The male differs by the shape of the conductor, the pointed tip of the terminal apophysis and the square median apophysis (Fig. 393).

Distribution. Doubtful from western Panama, Colombia to northern Argentina (Map 6).

Records. PANAMA: *Chiriquí Prov.* Volcán, 20 Feb. 1936, ♀ (W. J. Gertsch, AMNH). COLOMBIA: *Dept. Valle.* Río Jamundi, 9 Dec. 1969, 3♀, ♂ (W. Eberhard, MCZ); nr. Cali, 1,300 m, 15 Dec. 1971, ♀ (W. Eberhard, MCZ). *Meta.* Restropo, 1936, ♀ (J. Bequaert, MCZ); Mt. Redondo, 1,500 m, 71 km W Villavicencio, June 1947, ♀ (L. Richter, AMNH). BRAZIL: *Est. Pará.* Canindé, 1964, 2♀ (J. Carvalho, AMNH). *São Paulo.* Juquiá, 2♀ (F. Lane, MZSP). *Santa Catarina.* 3♀ (E. Reimoser, MCZ); Blumenau, ♀ (H. Leudenwaldt, MZSP). ARGENTINA: *Misiones Prov.* Eldorado, 1964, ♀ (A. Kovacs, AMNH); Puerto Victoria, 2♀ (Zenzes, MLP); Punta 17 de Octubre, 6♀ (MACN).

Micrathena molesta Chickering
Plates 1, 2; Figures 394–404; Map 6

Micrathena molesta Chickering, 1961: 441, figs. 127–132, ♀. Female holotype from Tablazo [Cerro Tablazo, San José Prov.], Costa Rica (MCZ), examined.

Description. Female from type locality. Carapace orange, darker on each side. Sternum orange. Legs orange-brown. Abdomen orange with sclerotized areas orange-brown; sides and venter orange-white with some black pigment on sides and behind spinnerets. Carapace with high thorax, three pairs of dimples and a round thoracic mark; without rims. Abdomen dorsally flattened with one pair of spines overhanging carapace, three spines posterolaterally on each side and four pairs on sides (Figs. 394, 395). Total length, 7.0 mm. Carapace, 2.3 mm long, 1.2 mm wide. First femur, 2.2 mm; patella and tibia, 2.3 mm; metatarsus, 1.3 mm; tarsus, 0.5 mm. Second patella and tibia, 1.9 mm; third, 1.2 mm. Fourth femur, 2.4 mm; patella and tibia, 1.9 mm; metatarsus, 1.4 mm; tarsus, 0.6 mm.

Male from Costa Rica. Carapace orange, sides black. Sternum, coxae orange-white. Legs orange-gray. Dorsum of abdomen white with black along each side, venter gray with black patch on each side and one behind spinnerets. Carapace with three pairs of dimples and thoracic mark. First coxa with small hook on posterior edge, second femur with groove. Abdomen with sides almost parallel, slightly convex (Fig. 402). Total length, 3.4 mm.

Carapace, 1.3 mm long, 0.9 mm wide. First femur, 1.3 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm. Second patella and tibia, 1.1 mm; third, 0.6 mm. Fourth femur, 1.4 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 4.8 to 6.4 mm, males from 3.2 to 3.6 mm. The spines are sometimes reduced in size, and the third pair, the second laterals, may be replaced by a small hump. The transverse bar of the epigynum is of variable width. In about half the females examined it had been torn off, leaving a stump of variable shape (Figs. 399–401). Unlike specimens from Costa Rica, the female collected in Chiriquí, Panama is heavily sclerotized and dark, with brown carapace and legs, black abdomen with a white pigment band on each side and, in between, a transverse white stripe broken in the middle and located behind the fourth lateral spines.

Note. Female and male have been collected at Tuis hill top, and a number of males and females come from Finca La Selva, Costa Rica.

Diagnosis. Unlike similar species with 14 to 16 spines, the transverse bar of the epigynum is straight, projecting, and lacks a posteromedian lobe (Fig. 396). It is the only *Micrathena* species in Central America that has the bar of the epigynum torn off, leaving behind a depression of variable outline in posterior view (Figs. 399–401).

The male can be separated from others of the *kirbyi* group with a coxal hook by the uneven outline of the tegulum (above the large median apophysis), by the projecting, sclerotized conductor forming a hook above the tip of the embolus, and by the shape of the paracymbium (Figs. 403, 404).

Natural History. Females had their webs in low vegetation in dense jungle at Turrialba (Plate 1).

Distribution. Nicaragua to western Panama (Map 6).

Records. NICARAGUA: Musawas, Waspuc Riv., ♂ (B. Malkin, AMNH). COSTA RICA: *Guanacasta Prov.* Tilarán, ♀ (MZCR). *Heredia.* Finca La Selva, nr. Puerto Viejo, 50 m, common, ♀, ♂ (MCZ). *Limón.* Waldeck Farm, ♀ (NMW); Hamburg Farm, 6♀ (NMW). *Cartago.* Turrialba, ♀♀ (AMNH, CAS, EPC, CUC); Navarro, ♀ (MZCR); Tuis, hill top, ♀, ♂ (MCZ). *San José.* San José, 5♀ (NMW); Braulio Carillo Natl. Park, 2♀ (MCZ). *Puntarenas.* Monteverde, 1,580 m, 3♀, ♂, imm. (MCZ). PANAMA: *Bocas del Toro Prov.* Corrietite Grandes, nr. Changuinola, ♀ (UPMI). *Chiriquí.* La Fortuna Dam site, Sept. 1976, ♀ (M. Robinson, MCZ).

Micrathena lenca new species
Figures 405–409; Map 6

Holotype. Female, three female paratypes from Catherinas [?=Catarinita, 15°54'N 92°54'W], Chiapas, 1,400 m el., 14–22 May 1942 (H. Wagner, AMNH), one paratype (MCZ). The specific name is a noun in apposition after the Indian tribe of the region.

Description. Female. Carapace orange, black on sides. Sternum, legs orange. Dorsum of abdomen white, without pigment

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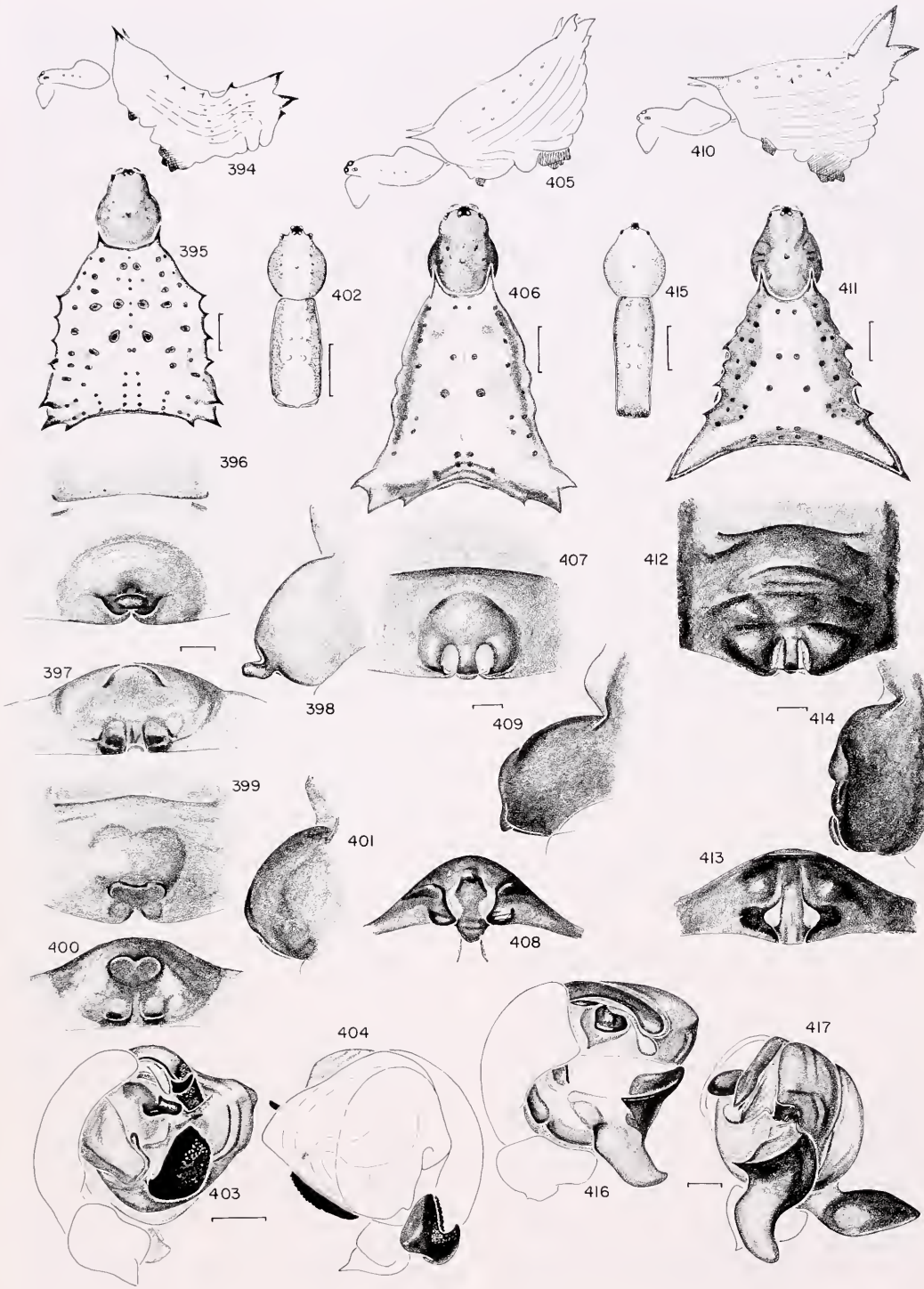
Figures 394–404. *Micrathena molesta* Chickering. 394–401. Female. 394. Lateral. 395. Dorsal. 396, 399. Epigynum, ventral. 397, 400. Epigynum, posterior. 398, 401. Epigynum, lateral. 399, 400, 401. Bar and lobe torn off. 402, 403. Male. 402. Dorsal. 403. Left palpus, mesal. 404. Palpus, lateral.

Figures. 405–409. *Micrathena lenca* n. sp., female. 405. Lateral. 406. Dorsal. 407. Epigynum, ventral. 408. Epigynum, posterior. 409. Epigynum, lateral.

Figures 410–417. *Micrathena tziscao* n. sp. 410–414. Female. 410. Lateral. 411. Dorsal. 412. Epigynum, ventral. 413. Epigynum, posterior. 414. Epigynum, lateral. 415–417. Male. 415. Dorsal. 416. Palpus, mesal. 417. Palpus, ventral.

Scale lines. 0.1 mm, except Figures 394, 395, 402, 405, 406, 410, 411, 415, 1.0 mm.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on sides and posteriorly; indistinct black patch on each side and on each side of posterior face of triple spine; sides with black pigment, venter orange with eight sclerotized areas darker orange. Carapace with three pairs of dimples, distinct thoracic depression and high thorax. Posterior median eyes 1.5 diameters of anterior medians; laterals slightly smaller than anterior median eyes. Abdomen subtrapezoidal with a pair of spines overhanging carapace anterior, and a posterolateral extension bearing three spines (Figs. 405, 406). Total length, 6.5 mm. Carapace, 2.3 mm long, 1.9 mm wide. First femur, 2.4 mm; patella and tibia, 2.5 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm. Second patella and tibia, 2.2 mm; third, 1.3 mm. Fourth femur, 2.6 mm; patella and tibia, 2.2 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm.

Diagnosis. This eight-spined species differs from all others by the globular epigynum having two light impressions posteriorly (Figs. 407, 409) and a sclerite on each side in posterior view (Fig. 408). The similar *M. tziscao* has 14 spines and differs in details of the epigynum.

Micrathena tziscao new species
Figures 410–417; Map 6

Types. Female holotype from Laguna Tziscao, Montobello, Chiapas [16°05'N, 91°40'W], Mexico with female, male and juvenile paratypes, 17–18 Aug. 1973 (P. Brignoli, MCZ). The species name is a noun in apposition after the type locality.

Description. Female. Carapace orange, gray on each side. Sternum, legs orange. Coxae slightly lighter than sternum. Dorsum of abdomen white with black edge on each side and posteriorly; sides and venter black with two indistinct light patches on each side of spinnerets. Carapace with three pairs of quite indistinct dimples and distinct thoracic depression; thorax high. Posterior median eyes slightly larger than others, which are subequal. Abdomen subtriangular with fourteen spines, two overhanging carapace in front, three pairs on sides, a pair of double spines posterolaterally with a small spine below (Figs. 410, 411). Total length, 6.7 mm. Carapace, 2.7 mm long, 2.0 mm wide. First femur, 2.6 mm; patella and tibia, 2.7 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm. Second patella and tibia, 2.4 mm; third, 1.4 mm. Fourth femur, 2.8 mm; patella and tibia, 2.4 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm.

Male. Carapace orange, gray on sides. Sternum, legs orange. Dorsum of abdomen whitish with black on sides and posterior edge; sides black (Fig. 415); venter with black posterior to spinnerets; anterior orange with some gray pigment. Posterior median eyes slightly larger than others; posterior laterals slightly smaller than anterior median eyes. First coxa with hook, second femur with groove proximally. Sides of abdomen almost parallel. Total length, 4.6 mm. Carapace, 1.7 mm long, 1.3 mm wide. First femur, 1.7 mm; patella and tibia, 1.9 mm; metatarsus, 1.0 mm; tarsus, 0.6 mm. Second patella and tibia, 1.6 mm; third, 0.9 mm. Fourth femur, 1.8 mm; patella and tibia, 1.4 mm; metatarsus, 1.0 mm; tarsus, 0.5 mm.

Note. It has been difficult to decide on the homology of sclerites around the embolus. The embolus is covered by a sclerotized terminal apophysis; below, proximally is a projecting sclerite that is probably part of the conductor (Fig. 416). The median apophysis lobe "hangs down" and resembles that found in the genus *Eustala* (Figs. 416, 417).

Diagnosis. Females differ from *M. lenca* by having 14 spines on the abdomen (Figs. 410, 411), and by the transverse swelling of the epigynum (Figs. 412–414). The unique shape of the median apophysis (Figs. 416, 417) separates the male from all others known.

Micrathena clypeata (Walckenaer)
Plate 2; Figures 418–425; Map 6

Epeira clypeata Walckenaer, 1805: 67. Specimens without locality, lost.
Acrosoma clypeatus:—C. L. Koch, 1838: 38, pl. 272, ♀.
Micrathena clypeata:—Reimoser, 1917: 90, pl. 2, fig.

3, ♀. Roewer, 1942: 955. Bonnet, 1957: 2864. Chickering, 1961: 400, figs. 14–20, ♀, ♂.

Micrathena planata Chamberlin and Ivie, 1936: 54, pl. 15, figs. 132, 133, ♀, ♂. Female holotype from Barro Colorado Island, Panama (AMNH), examined. First synonymized by Mello-Leitão, 1945b: 267.

Description. Female from Panama. Carapace, sternum orange. Legs dark brown. Abdomen orange-brown, lateral edges blackish, spines black. Carapace with three pairs of dimples and a circular thoracic depression. Dorsum of abdomen flat, with sclerotized disks and minute granulations, more distinct on venter; three thorns posteriorly on each side, and one on each lateral margin. Ring around spinnerets with anterior tubercle (Figs. 418, 419). Total length, 8.6 mm. Carapace, 3.4 mm long, 2.9 mm wide. First femur, 2.9 mm; patella and tibia, 3.2 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm. Second patella and tibia, 3.0 mm; third, 2.0 mm. Fourth femur, 3.2 mm; patella and tibia, 2.9 mm; metatarsus, 1.8 mm; tarsus, 0.7 mm.

Male. Coloration like female. Carapace with three pairs of dimples and a median thoracic depression (Fig. 423). First coxa with hook, second femur with groove. First leg with long macrosetae on first tibia, some longer macrosetae on second tibia; fourth femur with tubercles. Total length, 4.0 mm. Carapace, 1.9 mm long, 1.5 mm wide. First femur, 1.7 mm; patella and tibia, 1.8 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm. Second patella and tibia, 1.5 mm; third, 1.0 mm. Fourth femur, 1.5 mm; patella and tibia, 1.2 mm; metatarsus, 0.7 mm, tarsus, 0.4 mm.

Variation. Females vary in total length from 8.6 to 10.3 mm, males from 3.7 to 4.2 mm.

Note. Females and males have been collected together on Barro Colorado Island, Guyana and Suriname. The abdomen of half-grown females is like that of adults, with four spines on the edge of the flat abdomen.

Diagnosis. There are no other *Micrathena* females with a flat abdomen having four pairs of thorns along the edge (Figs. 418, 419). The male is distinguished by the large sclerotized prong of the median apophysis (Fig. 424), and the flat paracymbium (Fig. 425).

Natural History. Specimens have been collected in forest savanna in Guyana and in forest in Suriname. An orb measured in Suriname by D. Smith had a diameter of 22 cm and was 85 cm above the ground.

Distribution. Panama to Peru, Amazon drainage (Map 6).

Records. PANAMA: *Prov. Panamá.* Barro Colorado Island (many records); Pipeline Road. VENEZUELA: *Est. Aragua.* Rancho Grande, 4♀ (MACN). GUYANA: *Bartica Distr.* Kartabo, ♀ (CUC); Mackenzie, Demerara River, ♀ (CUC). Mazaruni, Pakaraima Mts., ♀ (CUC). Minnehaha Creek, ♀ (CUC). Canje, Ikuruwa Riv., 3♀, ♂ (MCZ). SURINAME: Zanderij Isl., ♀ (CUC). *Saramacca.* Voltzberg-Raleighvallen Res., 9♀, ♂ (MCZ). Moengo, Cottica River, ♀ (CUC). Gordua, ♀ (ZMB). Paramaribo, ♀ (ZMB). FRENCH GUIANA: St. Laurent de Maroni, 3♀ (PAN). COLOMBIA: *Est. Vaupés.* Río Vaupés, ♀ (AMNH). *Caquetá.* Río Orteguaza, 4♀ (AMNH). *Putumayo.* Río Putumayo, ca. Pto. Asis, ♀ (MCZ); San Antonio, Río Guamues, imm. (MCZ). *Nariño.* Barbacoas, ♀ (MCZ). ECUADOR: *Prov. Pichincha.* km 113 vía Pto. Quito, ♀, 3♂ (MECN). *Napo.* Río Napo, 2♀ (MCZ); R. F. Cuyabeno, 3♀ (MECN). PERU: *Dept. Amazonas.* Río Alto Marañón betw. Río Cenepa and Río Nieva, ♀ (AMNH). *Loreto.* Iquitos, 6♀ (MCZ). *San Martín.* Moyobamba, ♀ (AMNH). *Huánuco.* Divisoria, ♀ (AMNH); Cucharas, many ♀ (EPC). *Junín.* Amable María, ♀, ♂ (PAN). Río Bombo, Alto Tapiche, ♀ (AMNH). BRAZIL: *Est. Pará.* Canindé, Rio Gurupi, ♀ (AMNH); Cachoeira, ♀ (ICSP); Belém, 2♀ (MACN, NMW); Santarém, ♀ (NMW); Rio Tapajós, ♀ (INPA). *Amazonas.* Tefé, 2♀, ♂ (MCZ, IBSP); mouth of Rio Embira and Rio Jurua, ♀ (AMNH); 45 km N Manaus, ♀, ♂ (INPA); Manaus, 6♀, ♂ (MCZ, MZSP, IBSP, NRS, MEG); 20 km N Manaus, 2♀

(NRS); Rio Autás, Cururuzinho, 2♀ (NRS); Rio Negro, Umaritubo, 11♀ (NRS); Taracuá, ♀ (NRS); Rio Autás, Capiranga, ♀ (NRS); Lago Jacaré, Rio Solimões, 2♀ (MZSP). *Rondônia.* Pôrto Velho, 2♀ (MCZ); Abunã, ♀ (MCZ); Vila Murtinho, 3♀ (MCZ).

The *triangularispinosa* Group

The *triangularispinosa* group is characterized in both sexes by a shiny, dome-shaped carapace having only an indistinct thoracic mark (Figs. 432, 433, 471, 473, 498, 499). The abdomen of females is subtriangular in all species (except trapezoidal *M. schenkeli* and *M. ucayali*). All except *M. ornata* have four to eight spines; all have a large anterior pair of spines overhanging the carapace and a large pair of dorsal, posterior spines (Figs. 433, 449, 481, 509). In addition there may be a pair of usually small lateral spines and a pair of small posterior spines. The epigynum is a large bulge with a small posteromedian lobe or tip. There is no transverse bar. The opening is a slit on the posterior face, of variable shape in most species (Figs. 434–436, 458–463).

Males have a shiny, dome-shaped carapace like females and a short, rectangular to trapezoidal abdomen (Figs. 437, 477, 495), slightly wider behind than in front. All lack a hook on the first coxa and the corresponding groove on the second femur. The palpus has a relatively straight to slightly curved embolus. A lobe in the center of the median face is assumed to be the paramedian apophysis, and a characteristic median apophysis is present, consisting of two almost equal sized areas, one overlapping the other, and both weakly sclerotized (Figs. 7, 438, 467, 496; except in *M. acuta* and and *M. flaveola*, where the structure is simpler, Figs. 8, 504, 517). Secondarily some sclerites have been lost: the paramedian apophysis and the median apophysis.

Diagnostic features for females in the group are the number of abdominal spines, the shape of the sternum (Fig. 510), and the shape of the epigynum and its lobe. In males, diagnostic features are the shape of the paracymbium (Figs. 455, 468, 479, 520) and the shape of the median apophysis (Figs. 7, 438).

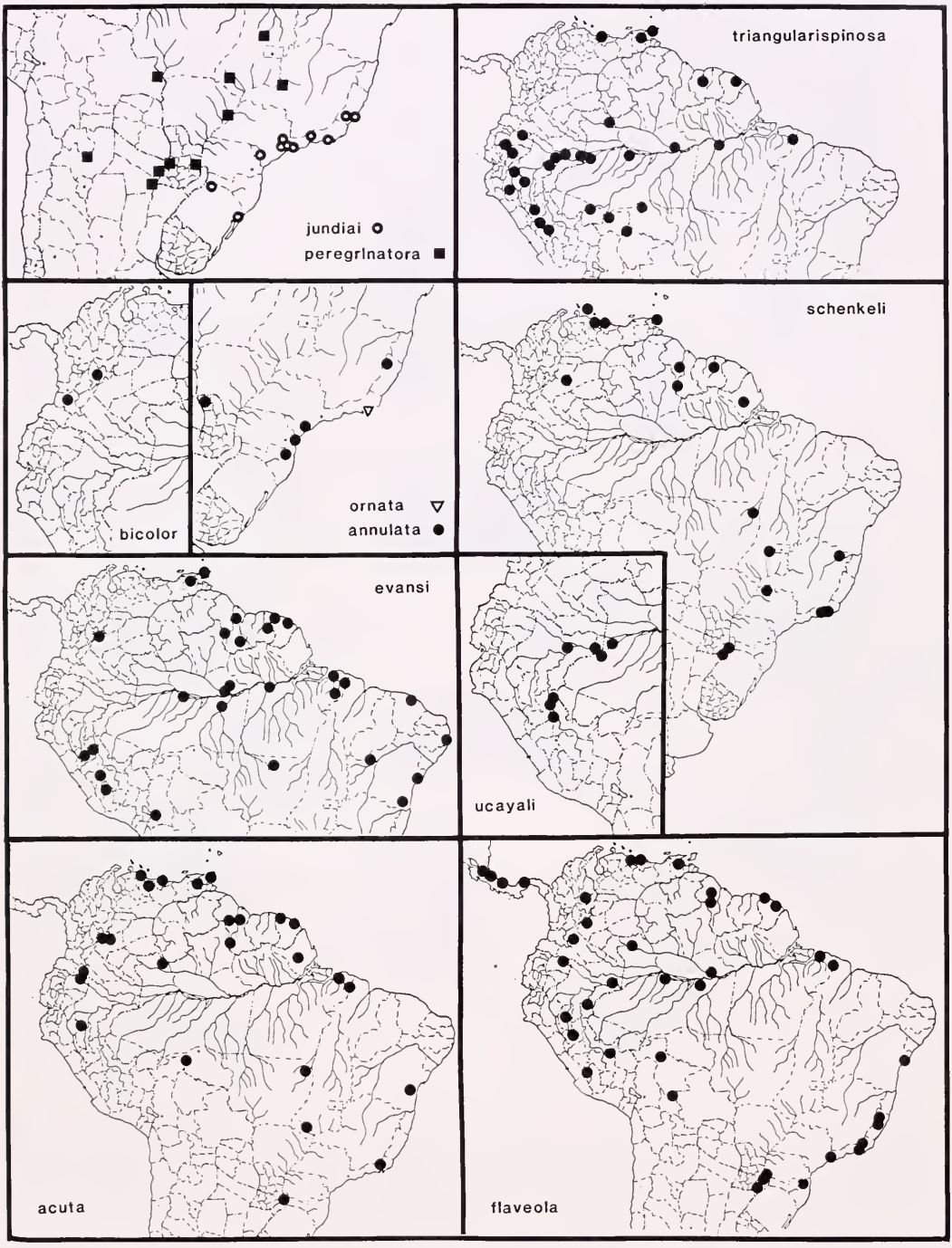
Key to the *triangularispinosa* Group

Females

1. Sternum dome-shaped, bulging (Fig. 510) 2
– Sternum flat 3
2(1) Six spines on abdomen (Figs. 498, 499); widespread, Map 7 ..... *acuta*
– Eight spines on abdomen (Figs. 508, 509); widespread, Map 7 ..... *flaveola*
3(1) Abdomen with only the four large spines (Figs. 426, 427); Est. Goiás, Brazil to northern Argentina, Map 7 ..... *peregrinatora*
– Abdomen with 6, 8 or 12 spines 4
4(3) Abdomen with 12 spines (Fig. 522); southeastern Brazil, Map 7 ..... *ornata*
– Abdomen with 6 or 8 spines 5
5(4) Abdomen with 6 spines (figs. 440, 441, 456, 457, 480, 481) 6
– Abdomen with 8 spines (Figs. 448, 449, 471, 472, 490, 491) 8
6(5) Abdomen with two pairs of relatively large posterior spines (Figs. 480, 481); epigynum tip a semicircular lobe (Fig. 482) often torn off (Fig. 485); widespread, Map 7 ..... *schenkeli*
– Abdomen with one pair of large posterior spines and a pair of tiny lateral spines 7
7(6) Epigynum tip tripartite (with two paraxial grooves, Fig. 434); southeastern Brazil, Map 7 ..... *jundiai*
– Epigynum tip entire, usually with a light central area on posterior face (Fig. 459); widespread, Map 7 ..... *evansi*
8(5) Anterior of epigynal bulge flat in profile (Fig. 452); Colombia, Map 7 ..... *bicolor*
– Epigynum with bulge rounded in profile (Figs. 476, 494) 9
9(8) Lower posterior spines almost as large as upper posterior spines (Figs. 490, 491); upper Amazon, Peru, Brazil, Map 7 ..... *ucayali*
– Lower posterior spines smaller than upper ones (Figs. 440, 441, 471, 473) 10
10(9) Epigynum in ventral view sculptured with two paraxial grooves (Fig. 442); southeastern Brazil, Paraguay, Map 7 ..... *annulata*
– Epigynum not so sculptured, with tiny lobe (Fig. 474); widespread, Map 7 ..... *triangularispinosa*

Males

Males of *M. ornata* and *M. peregrinatora* are unknown; male of *M. bicolor* uncertain association.



Map 7. Distribution of *Micrathena* species of the *triangularispinosa* group.

1. Tegulum of palpus bulging, extending distally (Figs. 504, 519) 2
– Tegulum without distal bulge (Figs. 438, 454) 3
2(1) Sculptured area of cymbium same size as facing paracymbium (Fig. 505); widespread, Map 7 ..... *acuta*
– Sculptured area of cymbium much larger than facing paracymbium (Figs. 8, 518, 520); widespread, Map 7 ..... *flaveola*
3(1) Cymbium with a proximal dorsal bulge (Figs. 488, 489); widespread, Map 7 ..... *schenkeli*
– Cymbium otherwise 4
4(3) Paramedian apophysis a narrow, curved lobe (Figs. 438, 446, 469) 5
– No such lobe present (Fig. 454); palpus as in Figures 454, 455 ..... suspected male of *bicolor*
5(4) Paracymbium pointed toward dorsum (Fig. 439); southeastern Brazil, Map 7 ..... *jundiai*
– Paracymbium otherwise 6
6(5) Paracymbium with a concave surface toward dorsum (Figs. 466, 468, 470); widespread, Map 7 ..... *evansi*
– Paracymbium otherwise 7
7(6) Paracymbium with a dorsal hook (Fig. 479); widespread, Map 7 ..... *triangularispinosa*
– Paracymbium otherwise 8
8(7) Paracymbium as in Figure 497; upper Amazon, Peru, Brazil, Map 7 ..... *ucayali*
– Paracymbium as in Figure 447; southeastern Brazil, Paraguay, Map 7 ..... *annulata*

Micrathena peregrinatora (Holmberg) Figures 426–431; Map 7

Acrosoma peregrinatorum Holmberg, 1883: 232. Probably immature female type from Formosa, Argentina, lost.

Micrathena peregrinatorum:—Reimoser, 1917: 152. Roewer, 1942: 961. Bonnet, 1957: 2873.

Description. Female. Carapace orange-brown with a median gray streak. Sternum white, framed by some gray pigment. Coxae darker; distal leg articles orange-brown with longitudinal dusky lines. Dorsum of abdomen with black and white patches, sides with dorsoventral lines of white patches with gray; venter white and gray patches. Carapace evenly domed, with indistinct thoracic depression. Abdomen triangular with four spines, two overhanging carapace and two posterior (Figs. 426, 427). Total length, 6.0 mm. Carapace, 2.4 mm long, 1.9 mm wide. First femur, 1.9 mm; patella and tibia, 1.9 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm. Second patella and tibia, 1.8 mm; third, 1.4 mm. Fourth femur, 2.5 mm; patella and tibia, 1.9 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm.

Variation. Females vary in total length from 5.7 to 5.9 mm. Some individuals have a minute pair of spines underneath the posterior ones.

Note. The male is unknown.

Diagnosis. The presence of only four spines (Figs. 426, 427) separates this species from all others of the *triangularispinosa* group.

Distribution. Southern Brazil to northern Argentina (Map 7).

Records. BRAZIL: *Est. Goiás.* Corumbá, Aug. 1952, ♀ (F. Lane, MZSP); Jataí, Oct. 1962, 4♀ (Exp. MZSP). *Minas Gerais.* Cachoeira do Marimbondo, 4 March 1965, ♀ (Vizotto, MZSP). *Mato Grosso do Sul.* Três Lagoas, Nov. 1966, ♀ (F. Lane, MZSP), 28 July 1965, ♀ (K. Lenko, MZSP). PARAGUAY: 1891–1893, ♀ (Dr. Bohls, BMNH). *Dept. Central.* Aregua, 18 Feb. 1982, ♀ (B. Barrios, JAK). *Alto Paraná.* Taguarazapa, imm. (AMNH). ARGENTINA: *Prov. Salta.* Salta, 1907, 2♀ (E. Rei-

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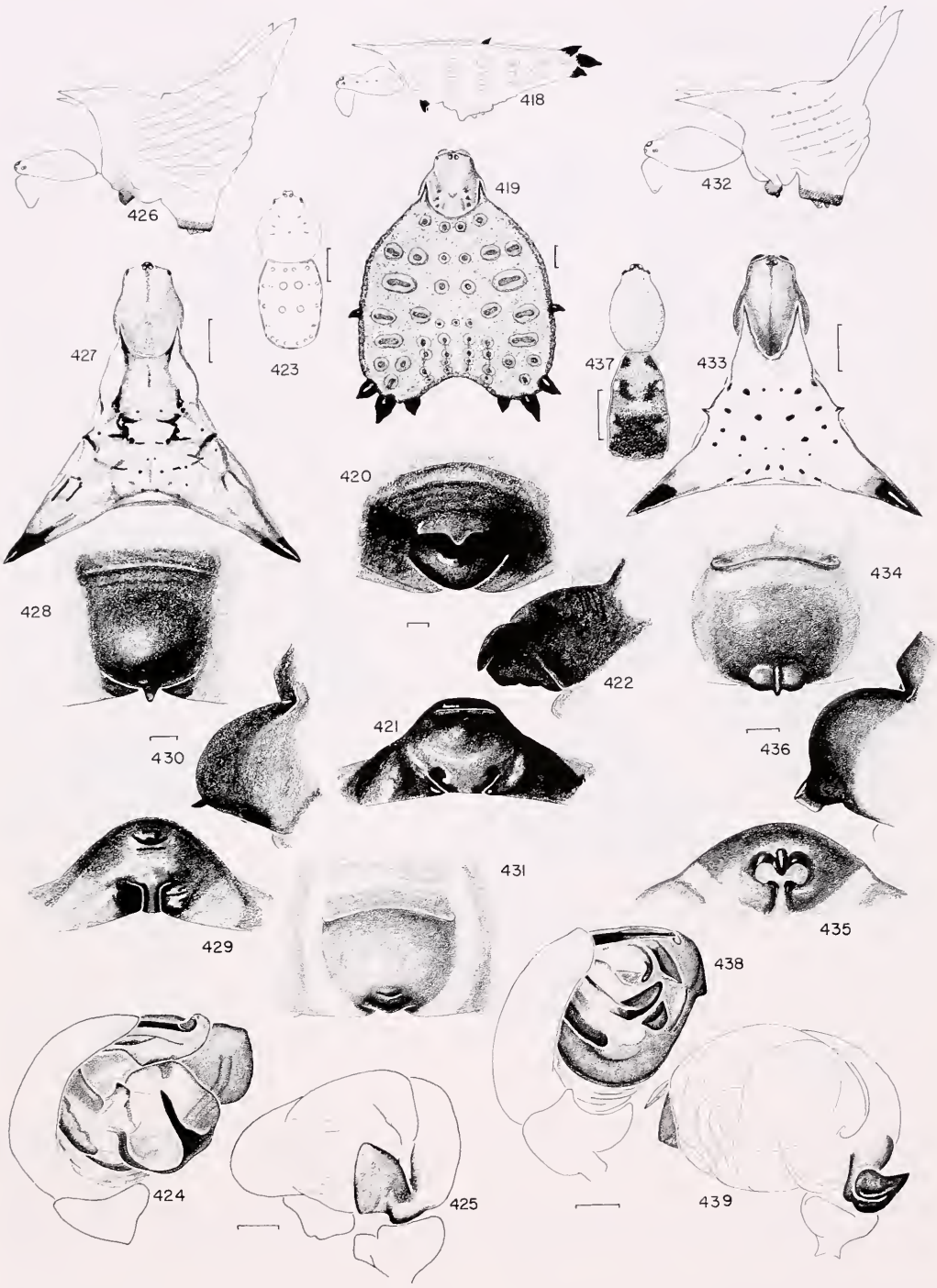
Figures 418–425. *Micrathena clypeata* (Walckenaer). 418–422. Female. 418. Lateral. 419. Dorsal. 420. Epigynum, ventral. 421. Epigynum, posterior. 422. Epigynum, lateral. 423–425. Male. 423. Dorsal. 424. Left palpus, mesal. 425. Palpus, lateral.

Figures 426–431. *Micrathena peregrinatora* (Holmberg), female. 426. Lateral. 427. Dorsal. 428. Epigynum, ventral. 424. Epigynum, posterior. 430. Epigynum, lateral. 431. Epigynum with lobe torn off.

Figures 432–439. *Micrathena jundiai* n. sp. 432–436. Female. 432. Lateral. 433. Dorsal. 434. Epigynum, ventral. 435. Epigynum, posterior. 436. Epigynum, lateral. 437–439. Male. 437. Dorsal. 438. Palpus, mesal. 439. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 418, 419, 423, 426, 427, 432, 433, 437, 1.0 mm.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moser, NMW). *Chaco.* Resistencia, July 1934, ♀ (Hayward, MZSP).

Micrathena jundiai new species
Figures 432–439; Map 7

Holotype. Female and immature paratype from São Paulo [Enenheiro Marsilac, Est. São Paulo], Brazil, 27 Nov. 1960 (no. 8307, MZSP). The name is a noun in apposition after Jundiai, a collecting site near São Paulo.

Description. Female. Carapace yellow, darker in midline and on sides. Sternum white with black line on each side. Coxae yellowish. Legs yellowish, distally brown with darker longitudinal streaks. Dorsum of abdomen whitish; posterior dorsal spines black; venter with black patch between epigynum and spinnerets; sclerotized areas brown. Carapace without thoracic depression. Posterior median eyes twice diameter of anterior medians; anterior laterals 1.2 diameters; posterior laterals subequal to anterior median eyes. Abdomen subtriangular with six spines (Figs. 432, 433). Total length, 5.3 mm. Carapace, 2.2 mm long, 1.7 mm wide. First femur, 2.0 mm; patella and tibia, 2.2 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm. Second patella and tibia, 1.9 mm; third, 1.2 mm. Fourth femur, 2.6 mm; patella and tibia, 1.9 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm.

Male from Rio de Janeiro. Carapace, sternum dark brown. Sternum with orange transverse mark anteriorly. Coxae orange, distal articles of legs brown. Dorsum of abdomen orange-brown with five white spots and indistinct black patches; venter black. Carapace smooth without depression. Posterior median eyes twice the diameter of anterior medians; laterals subequal to anterior median eyes. No coxal hook. Abdomen trapezoidal (Fig. 437). Total length 3.9 mm. Carapace, 1.8 mm long, 1.1 mm wide. First femur, 1.3 mm; patella and tibia, 1.2 mm; metatarsus, 0.7 mm; tarsus, 0.5 mm. Second patella and tibia, 1.0 mm; third, 0.8 mm. Fourth femur, 1.4 mm; patella and tibia, 1.2 mm; metatarsus, 0.8 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 5.3 to 7.0 mm, males from 3.2 to 4.2 mm.

Note. Males and females have been collected together at several localities.

Diagnosis. The female is separated from other six-spined species by the sculpturing of the epigynum (Figs. 434, 435). *Micrathena annulata*, with similar sculpturing, has eight spines.

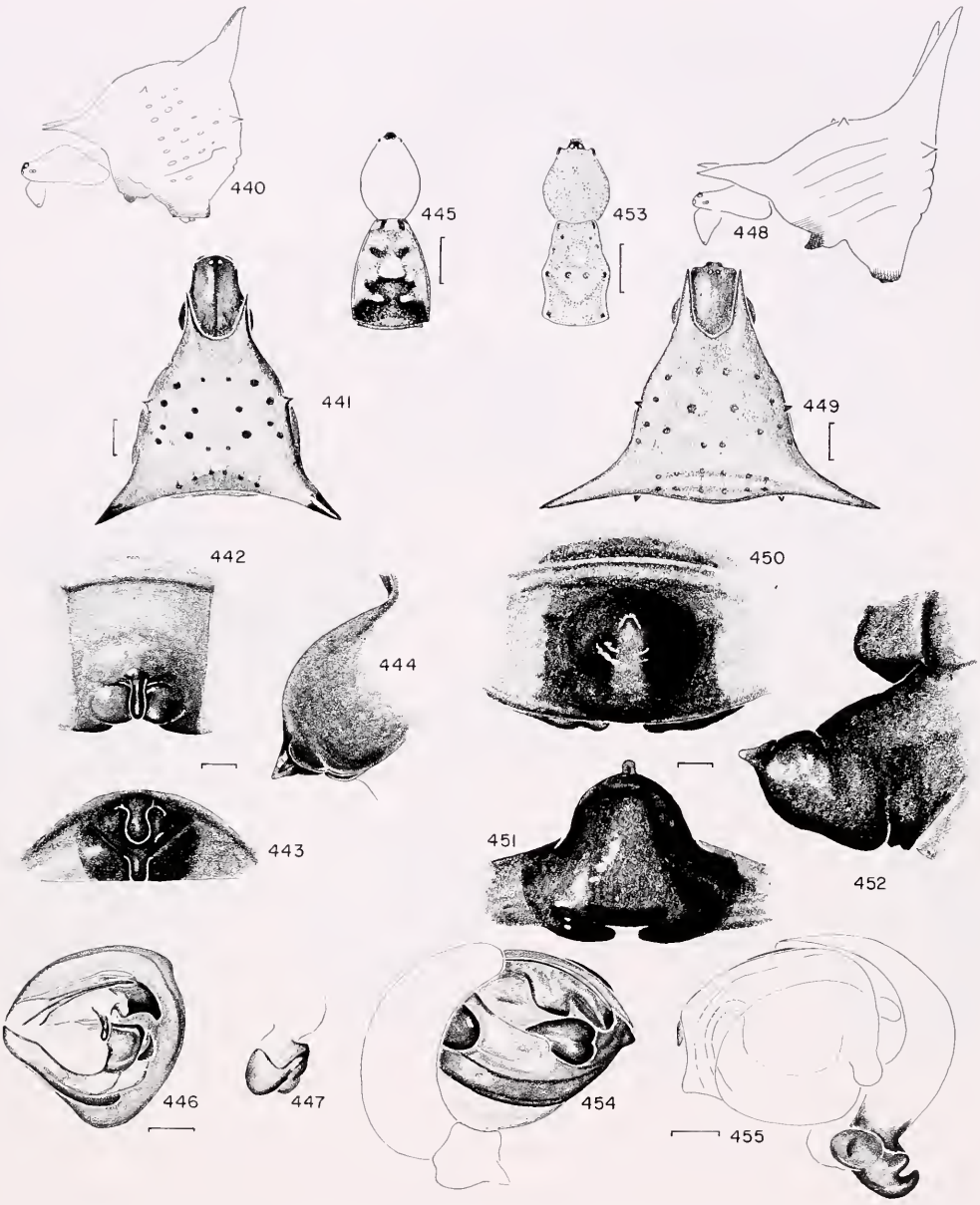
Distribution. Southeastern Brazil (Map 7).

Paratypes. BRAZIL: *Est. Espírito Santo.* Castelo, Nov. 1976, 2♂ (M. Alvarenga, AMNH); Guarapari, 12 Oct. 1943, ♂ (Soares, MZSP). *Rio de Janeiro.* Floresta dos Macacos, April 1961, 2♂ (M. Alvarenga, AMNH); Sumare, 200–300 m, Feb. 1946, 3♀ (H. Sick, AMNH); Paineiras, 30 March 1983, ♀ (H. and L. Levi, MCZ); Represa Rio Grande, Feb. 1976, ♂ (M. Alvarenga); Itatiáia, Dec. 1966, ♀ (H. Reichardt, MZSP). *São Paulo.* Itu, 2 Feb. 1959, ♀, ♂ (F. Lane, AMNH); Caraguatatuba, May 1962, ♀ (MZSP); Salesópolis, 1 Feb. 1961, ♀, ♂ (K. Lenko, MZSP); Jundiai, Nov. 1976, ♀ (A. Schneble, MCZ); Iporanga, 1 Nov. 1961, ♀, ♂ (Lenko and Reinhardt, MZSP); Ilho São Sebastião, 1 Feb. 1952, ♂ (Werner, MZSP); São Paulo, 27 Nov. 1960, ♀ (Werner, MZSP); São Sebastião, 3 June 1961, 2♀ (K. Lenko, MZSP). *Rio Grande do Sul.* Torres, 21 Nov. 1976, ♂ (A. Lise, FZRS); Iraí, 20 Nov. 1975, 7♀, ♂, imm. (A. Lise, FZRS).

Micrathena annulata Reimoser
Figures 440–447; Map 7

Micrathena annulata Reimoser, 1917: 149, pl. 9, fig. 31, ♀. Roewer, 1942: 953. Bonnet, 1957: 2861. Nine female, one juvenile syntypes from Est. Santa Catarina, Brazil (ZMW), examined. Roewer, 1942: 653. Bonnet, 1957: 2861.

Description. Female from Paraguay. Carapace, head dark brown, thoracic area with median narrow longitudinal dark band; posterior and sides of thorax dark brown; other areas lighter brown. Sternum brown. Legs brown with longitudinal dark, dusky stripes on tibiae. Dorsum of abdomen yellow-white, posterior spines black; venter black. Carapace high, shiny,



Figures 440–447. *Micrathena annulata* Reimoser. 440–444. Female. 440. Lateral. 441. Dorsal. 442. Epigynum, ventral. 443. Epigynum, posterior. 444. Epigynum, lateral. 445–447. Male. 445. Dorsal. 446. Left palpal bulb, mesal. 447. Paracymbium, mesal.

Figures 448–455. *Micrathena bicolor* (Keyserling). 448–452. Female. 448. Lateral. 449. Dorsal. 450. Epigynum, ventral. 451. Epigynum, posterior. 452. Epigynum, lateral. 453–455. Male. 453. Dorsal. 454. Palpus, mesal. 455. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 440, 441, 445, 448, 449, 453, 1.0 mm.

evenly curved, without any depression. Abdomen with one small spine on each side between anterior and posterior spines and one pair below posterior spines (Figs. 440, 441). Total length, 6.3 mm. Carapace, 2.4 mm long, 1.9 mm wide. First femur, 2.2 mm; patella and tibia, 2.2 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm. Second patella and tibia, 2.1 mm; third, 1.4 mm. Fourth femur, 2.7 mm; patella and tibia, 2.2 mm; metatarsus, 1.5 mm; tarsus, 0.7 mm.

Male. Carapace dark brown. Sternum with black and white pigment. Coxae colorless; distal leg articles darker. Dorsum of abdomen spotted white. Carapace domed, without thoracic mark. No coxal hook. Total length, 4.1 mm. Carapace, 1.9 mm long, 1.2 mm wide. First femur, 1.4 mm; patella and tibia, 1.4 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm. Second patella and tibia, 1.3 mm; third, 0.9 mm. Fourth femur, 1.7 mm; patella and tibia, 1.4 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 4.8 to 6.3 mm.

Note. The only male in collection was with six immatures, and had both palps expanded, thus drawings could be made only of the bulb without cymbium (Fig. 446), and of the paracymbium (Fig. 447), these perhaps not in comparative positions.

Diagnosis. This species can be separated from others of the *triangularispinosa* group with eight spines by the sculpturing of the epigynum (Figs. 442, 443), which is like that of the six-spined *M. jundiai.* The paracymbium of the male (Fig. 447) is distinct.

Distribution. Southern Brazil (Map 7).

Records. BRAZIL: *Est. Espírito Santo.* Rio São José, 14 Sept. 1942, ♀ (B. Soares, MZSP). *São Paulo.* Juquiá, 21–26 Aug. 1949, 6 imm., ♂ (F. Lane, MZSP). *Paraná.* Paranaguá, ♀ (MNRJ). PARAGUAY: *Concepción.* Territory Foncière, 2♀ (E. Reimoser, MCZ).

Micrathena bicolor (Keyserling) Figures 448–455; Map 7

Acrosoma bicolor Keyserling, 1863: 73, pl. 2, fig. 6. Two female syntypes from Bogotá, Colombia (BMNH), examined. 1892: 20, pl. 1, fig. 16, ♀.

Micrathena caucaensis Strand, 1908: 4. Female holotype from Popayán, Dept. Cauca, Colombia (SMF), examined. NEW SYNONYMY.

Micrathena bicolor:—Reimoser, 1917: 151. Bonnet, 1957: 2862.

Synonymy. Strand's specimen appears to be the only other female of *M. bicolor* in collections.

Description. Female. Carapace brown; sides of thorax yellow-brown; sternum black. Legs yellow, distal articles brown. Dorsum of abdomen yellow, without any black or white pigment spots; sides with black longitudinal bands along grooves, broken by yellow ridges; venter with black band having almost parallel sides, from pedicel to spinnerets. Sclerotized area of spinnerets brown-black. Carapace high and shiny, without thoracic depression. Abdomen with eight spines (Figs. 448, 449). Total length, 6.5 mm. Carapace, 2.5 mm long, 2.2 mm wide. First femur, 2.3 mm; patella and tibia, 2.4 mm; metatarsus, 1.5 mm; tarsus, 0.7 mm. Second patella and tibia, 2.2 mm; third, 1.6 mm. Fourth femur, 3.2 mm; patella and tibia, 2.6 mm; metatarsus, 1.8 mm; tarsus, 0.8 mm.

Male from Peru. Carapace shiny dark

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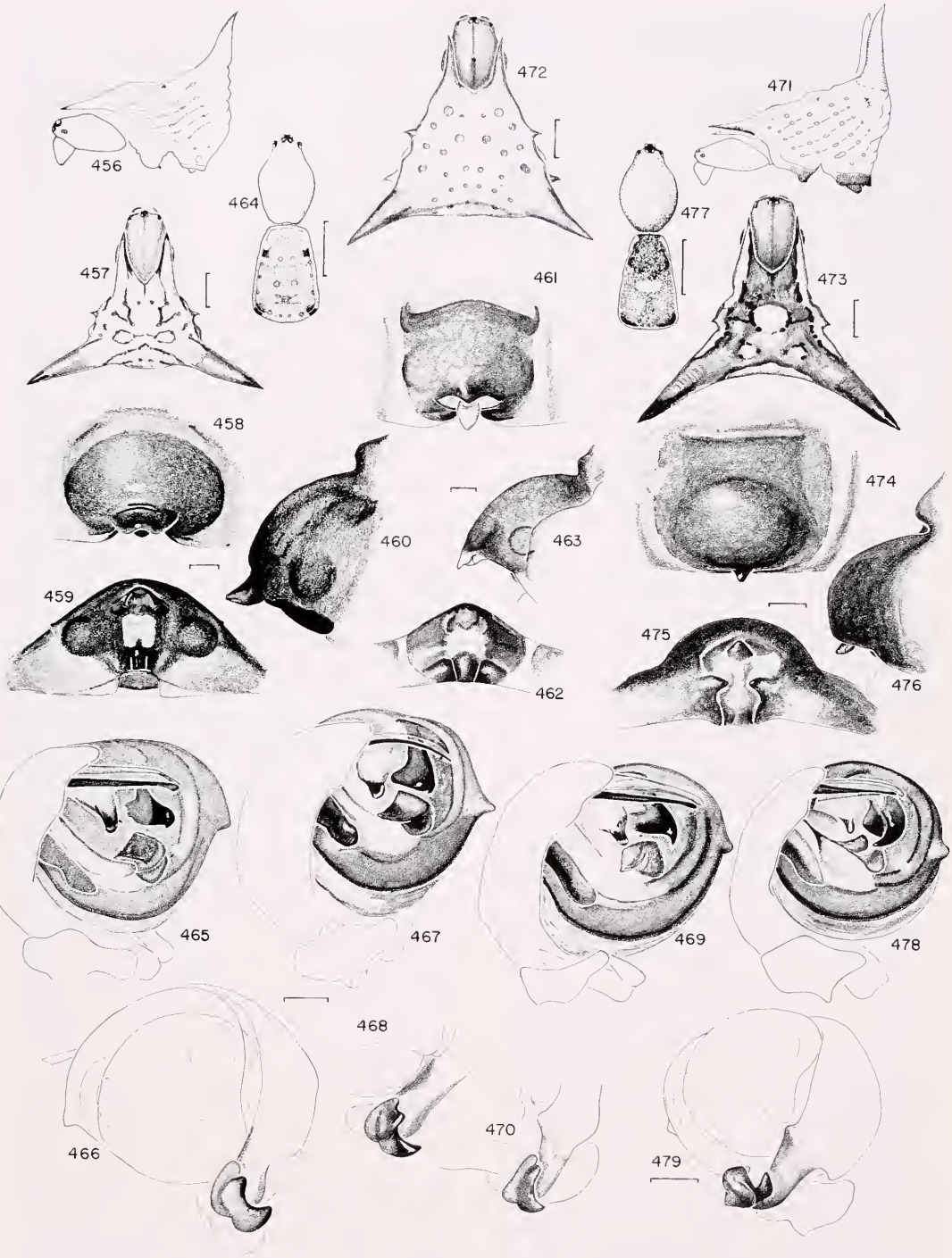
Figures 456–470. *Micrathena evansi* Chickering. 456–463. Female. 456. Lateral. 457. Dorsal. 458, 461. Epigynum, ventral. 459, 462. Epigynum, posterior. 460, 463. Epigynum, lateral. 458–460. (Trinidad, West Indies). 461–463. (Tefé, Brazil; doubtful if *M. evansi*). 464–470. Male. 464. Dorsal. 465, 467, 469. Left palpus, mesal. 466. Palpus, lateral. 468, 470. Paracymbium, lateral. 465, 466. (Santarém, Brazil). 467, 468. (Trinidad, West Indies). 469, 470. (Huánuco, Peru).

Figures 471–479. *Micrathena triangularispinosa* (De Geer). 471–476. Female. 471. Lateral. 472, 473. Dorsal. 474. Epigynum, ventral. 475. Epigynum, posterior. 476. Epigynum, lateral. 477–479. Male. 477. Dorsal. 478. Palpus, mesal. 479. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 456, 457, 464, 471–473, 477, 1.0 mm.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brown, with lighter median line posteriorly. Sternum orange with black and white pigment marks. Legs brown. Dorsum of abdomen orange-brown with lighter triangular area, round lighter area anterior to it, and black paired marks on sides (Fig. 453); sides black, venter light orange-brown. Carapace with indistinct thoracic mark, evenly curved. First coxa without hook. Sides of abdomen slightly wavy (Fig. 453). Total length, 3.9 mm. Carapace, 1.9 mm long, 1.2 m wide. First femur, 1.1 mm; patella and tibia, 1.2 mm; metatarsus, 0.6 mm; tarsus, 0.4 mm. Second patella and tibia, 1.0 mm; third, 0.7 mm. Fourth femur, 1.4 mm; patella and tibia, 1.0 mm; metatarsus, 0.7 mm; tarsus, 0.4 mm.

Note. The placement of the male with *M. bicolor* is uncertain. Both come from intermediate altitudes.

Diagnosis. This species differs from all others by the extreme bulge of the epigynum, best seen in profile (Fig. 452), having its anterior face flat and at right angles to the body axis.

Record. PERU: *Dept. Junín.* Amable María, ♂ (K. Jelski, PAN).

Micrathena evansi Chickering
Figures 456–470; Map 7

Micrathena evansi Chickering, 1960c: 77, figs. 41–45, ♂. Male holotype from Santarém forest, Est. Pará, Brazil (BMNH), examined.

? *Micrathena insolita* Chickering, 1961: 428, figs. 94–98, ♀. Juvenile female holotype from Portobello, Panama (MCZ), examined. DOUBTFUL NEW SYNONYMY.

Micrathena lepida Chickering, 1964: 264, figs. 30–34, ♀. Female holotype from Port of Spain, Trinidad, Lesser Antilles (MCZ), examined. NEW SYNONYMY.

Micrathena levii Chickering, 1964: 267, figs. 35–40, ♂. Male holotype from Simla, Trinidad, Lesser Antilles (AMNH), examined. NEW SYNONYMY.

Synonymy. No older name has been found for this species. *Micrathena lepida* is the female of *evansi* (Figs. 465, 466, illustrated from holotype); *M. levii* (Figs. 467, 468, illustrated from holotype) has a similar paracymbium; the differences of other sclerites in the palpus are probably due to geographic variation.

Micrathena insolita is not a recently molted adult, as Chickering thought, but an immature. Last instar immatures in this group have often a small tip in the epigynal area, of the size of this individual's. It has also small, very weakly sclerotized seminal receptacles. This might be an immature of *M. evansi*, but there are several related six-spined species. Only collecting at the type locality and finding adults will ascertain the synonymy.

Description. Female. Carapace, legs orange-brown. Sternum white. Dorsum of abdomen white with tip of spines black. Carapace high, domed. Abdomen with two anterior spines overhanging carapace, two posterolateral spines and a small spine on each side in between (Figs. 456, 457). Total length, 5.4 mm. Carapace, 2.3 mm long, 1.7 mm wide. First femur, 2.2 mm; patella and tibia, 2.0 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm. Second patella and tibia, 1.9 mm; third, 1.2 mm. Fourth femur, 2.7 mm; patella and tibia, 2.0 mm; metatarsus, 1.9 mm; tarsus, 0.6 mm.

Male from Trinidad. Carapace orange-brown, sternum lighter orange with some black pigment. Legs orange-brown. Dorsum of abdomen with white spots and black patches. Carapace without thoracic mark. First coxa without hook. Abdomen trapezoidal, curved posteriorly (Fig. 464). Total length, 3.9 mm. Carapace, 1.8 mm long, 1.2 mm wide. First femur, 1.2 mm; patella and tibia, 1.2 mm; metatarsus, 0.6 mm; tarsus, 0.4 mm. Second patella and tibia, 1.1 mm; third, 0.7 mm. Fourth femur, 1.4 mm; patella and tibia, 1.0 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm.

Variation. Total length of females varied from 4.9 mm to 7.2 mm, males from 3.4 to 4.0 mm. Some specimens have an indistinct thoracic mark. Most females have an epigynum as in Figures 458–460. A few females have a pointed tip (Fig. 461) and were first thought to be a distinct species until intermediates were found. Does the scape break off in some, or is it

just absent? Considerable variation in the shape of seminal receptacles prevented the use of this character to separate specimens with truncate tip of the epigynum from those with pointed tip. Some females have a small tubercle or minute spine below the large posterolateral spine on the abdomen. Are they hybrids of *triangularispinosa*? Individual sclerites on the conductor and median apophysis of male palpi are also quite variable in shape (Figs. 465, 467, 469), but the paracymbium is similar (Figs. 466, 468, 470).

Note. Male and female have been collected together by M. E. Galiano in Belém. For a while it was thought the male belonged to *M. triangularispinosa,* but males and females of *M. evansi* are common in Trinidad; *M. triangularispinosa* are not.

Diagnosis. Micrathena evansi females differ from other species with an arched carapace and flat sternum by having only six abdominal spines. Also, there is usually a light patch behind the truncate to pointed tip on the epigynum (Fig. 459). Males can be separated from those of *M. triangularispinosa* by the concave side of the paracymbium (Figs. 466, 468, 470).

Natural History. The species has been collected in forest savanna in Guyana and in forest at Belém.

Distribution. Trinidad, widespread in South America (Map 7).

Records. LESSER ANTILLES: *Trinidad.* Mt. St. Benedict, ♀ (AMNH); Maracas Valley, 3♀ (AMNH, BMNH); Port of Spain, 2♀ (MCZ). VENEZUELA: *Est. Monagas.* Caripito, sev. 3♀, ♂ (AMNH). GUYANA: Canje Ikuruwa River, ♀, ♂ (AMNH); nr. Yupukari, Rupununi Riv., ♀ (AMNH); Essequibo River, ♀ (BMNH). SURINAME: *Marowijne Distr.* Benzdorp, Lawa River, ♂ (AMNH). FRENCH GUIANA: St. Laurent de Maroni, 7♀ (PAN); Cayenne, 4♂ (PAN), 2♀ (MCZ). COLOMBIA: *Dept. Meta.* Villavicencio, 9♀ (AMNH). PERU: *Dept. Huánuco.* nr. Pucallpa, ♀ (AMNH); 80 km NE of Huánuco, 3,000 m, ♂ (CAS). *Junín.* Amable María, 3♂ (PAN). *Ayacucho.* Monterrico, 2♀ (PAN). BRAZIL: *Est. Pará.* Canindé, Rio Gurupi, 10♀ (AMNH); Belém, 9♀, 2♂ (MNRJ, MCZ); Jacare-Acanga, ♀ (AMNH); Santarém, 9♀ (BMNH); forest, Santarém, 8♀ (BMNH); km 305 Rodovia Belém-Brasília, 3°10′S, 47°30′W, 8♀ (MZSP). *Amazonas.* Rio Autaz, Capiranga, 2♀ (NRS); Manaus, Reserva Ducke, ♂ (MEG); 30 km NE Manaus, ♀ (INPA); Tefé (BMNH); Rio Autás, Sa. Amelia, ♂ (NRS); Umarituba, Rio Negro, ♀ (NRS). *Ceará.* ♀ (MCZ). *Pernambuco.* Mamanguape, ♀ (MZSP). *Mato Grosso.* Xingu, Jacare, 8♀ (AMNH). *Bahia.* Salvador, ♂ (AMNH); Uruçuca, 2♀ (FZRS); Camacari, ♀ (FZRS); Itamarajá, ♀ (FZRS). *Espírito Santa.* Sooretama [?], ♀ (MZSP). BOLIVIA: *Dept. La Paz.* Chulmani, 1,700 m, Tungas, 2♀ (MCZ).

Micrathena triangularispinosa (De Geer) Figures 471–479; Map 7

Aranea triangularispinosa De Geer, 1778: 321, pl. 39, figs. 9, 10, ♀. Female from Suriname (NRS), examined.

Acrosoma rufa Taczanowski, 1873: 265, pl. 5, fig. 20, ♀. Female holotype from Cayenne, French Guiana (PAN), examined. NEW SYNONYMY.

Acrosoma acutoides Taczanowski, 1879: 114, pl. 1, fig. 31, ♀. Female holotype from Amable María [Dept. Junín], Peru (PAN), examined. NEW SYNONYMY.

Micrathena perlata:—Simon, 1895: 852. Male paralectotype here designated (not lectotype), from São Paulo de Olivença [Est. Amazonas, Brazil] (no. 244, MNHN), examined.

? *Micrathena mathani* Simon, 1897b: 468. Female from São Paulo de Olivença [Amazonas, Brazil] and Pebas, Peru (MNHN), lost. NEW SYNONYMY.

Micrathena dahli Reimoser, 1917: 150, pl. 9, fig. 32, ♀. Four female syntypes from Caracas, Venezuela (two damaged) (NMW), examined. Roewer, 1942: 956. Bonnet, 1957: 2865. NEW SYNONYNY.

Micrathena acutoides:—Roewer, 1942: 953. Bonnet, 1957: 2861.

Micrathena munsonae Archer, 1971: 158, fig. 8, ♀. Female holotype from Moyobamba, Peru (AMNH), examined. NEW SYNONYMY.

Micrathena spinosa:—Roewer, 1942: 964 (in part). Bonnet, 1957: 2879 (in part).

Synonymy. A pinned specimen of De Geer's *triangularispinosa* was found in the

Natural History Museum, Stockholm. Most of the exoskeleton of the abdomen, including the venter of the epigynum, appeared to have been nibbled away be dermestid beetles. It was carefully placed into detergent and then into alcohol, but unfortunately fell apart. The shape of the carapace, sternum and seminal receptacles still visible make it fairly certain that it is this species. Linnaeus' *A. spinosa* is not the same, as thought by Reimoser and others, since *A. spinosa* is described by Linnaeus as having eight dorsal spines, the last pair extending posteriorly. *Micrathena mathani* is described as having a flat sternum and eight abdominal spines; *M. dahli* also has eight spines. Both are this species.

Description. Female from Peru. Carapace orange-brown with median dark line, sides dark. Sternum orange with white pigment. Femora of legs orange, distal articles black. Abdomen, dorsum white or with black pigment (Figs. 472, 473); sides with black grooves, forming black lines; venter with dark brown sclerotized areas. Carapace evenly domed. Abdomen with two anterior spines overhanging carapace, two large posterolateral spines, and small spine in between on each side; posteriorly, another pair of smaller spines below large spine (Figs. 471, 472). Total length, 5.5 mm. Carapace, 2.0 mm long, 1.6 mm wide. First femur, 2.0 mm; patella and tibia, 2.0 mm; metatarsus, 1.2 mm; tarsus, 0.7 mm. Second patella and tibia, 1.7 mm; third, 1.2 mm. Fourth femur, 2.5 mm; patella and tibia, 1.8 mm; metatarsus, 1.3 mm; tarsus, 0.7 mm.

Male from Est. Pará, Brazil. Carapace, legs dark brown, sternum brown. First two pairs of coxae brown, third and fourth yellow-white. Dorsum of abdomen black with a median white patch and several pairs of light patches; venter black. Carapace with very indistinct shallow thoracic mark. Coxal hook absent. Abdomen trapezoidal, sides slightly convex (Fig. 477). Total length, 3.8 mm. Carapace, 1.8 mm long, 1.2 mm wide. First femur, 1.2 mm; patella and tibia, 1.2 mm; metatarsus, 0.6 mm; tarsus, 0.4 mm. Second patella and tibia, 1.0 mm; third, 0.7 mm. Fourth femur, 1.4 mm; patella and tibia, 1.1 mm; metatarsus, 0.7 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 5.0 to 6.9 mm, males from 3.8 to 3.9 mm. Females often have a contrasting pattern on the abdomen (Fig. 473); sometimes this is absent. The sternum may be white or brown. The tip of the epigynum is quite variable; it is always subtriangular and located on the posterior slope of the bulge. Sometimes the tip has a slight ridge; sometimes it is minute or completely absent (perhaps torn off).

Note. Females have been collected with males in Manaus by M. E. Galiano (but also with a male of *M. evansi*). Males and females have also been collected in the Monsón Valley, Peru.

Diagnosis. This eight-spined species differs from *M. flaveola* by the flat sternum, and from *M. evansi* by having one more pair of spines, and in the structure of the epigynum (lacking a light area on the posterior face). The paracymbium of the male is more complex than that of *M. evansi*: it lacks the concave surface (Fig. 479), and the curved conductor encloses a sclerotized dark structure (Fig. 478), not present in *M. evansi.*

Distribution. Trinidad to Bolivia (Map 7).

Records. LESSER ANTILLES: *Trinidad.* ♀ (MCZ). VENEZUELA: *Est. Monagas.* Caripito, ♀ (AMNH). GUYANA: *Bartico Distr.* Kartabo, ♀ (CUC). SURINAME: *Saramacca.* Voltzberg-Raleighvallen Nature Res., 2♀ (MCZ). FRENCH GUIANA: Cayenne, ♀ (PAN). COLOMBIA: *Dept. Amazonas.* Leticia, ♀ (CNC). ECUADOR: *Prov. Napo.* R. F. Cuyabeno, ♀ (MECN). *Tungurahua.* Río Topo, 5♀, 3 juv. (EPC). *Morena-Santiago.* Taisha, 530 m, ♀ (MCZ). *Pastaza.* Yacu, 900 m, ♀ (MCZ). PERU: *Dept. Loreto.* Iquitos, 9♀ (AMNH, MCZ); Estiron, Río Ampiacu, ♀ (AMNH); Río Samiria, ♀ (AMNH). *San Martín.* 2 km NE Moyobamba, Mishquiyacu, 1,600 m, 12 ♀, 2 imm. (AMNH).

Amazonas. Río Alto Marañón betw. Río Campa and Río Nieva, ♀ (AMNH). *Cajamarca*. Pacanga, ♀ (BMNH). *Huánuco*. Tingo María, 18♀ (AMNH, EPC); Monsón Valley, Tingo María, ♀, ♂ (CAS); Huallaga River, 600 m, ♀ (EPC); Cucharas, Huallaga Valley, 9♀, 2 imm. (EPC); Divisoria, ♀ (AMNH). *Pasco* [?]. Cam. del Pechis [? Cam. al Pichis, Pasco, 10°58′S, 75°13′W], ♂ (CUC). *Junín*. Valle Chanchamayo, 800 m, ♀ (EPC). *Madre de Dios*. Iberia, ♂ (AMNH). BRAZIL: *Est. Amazonas*. Igarape Belém, nr. confluence with Rio Solimões, ♀ (AMNH); Manaus, 2♀, 2♂ (MEG); Tefé, 2♀ (BMNH, MCZ); Umarituba, Rio Negro, ♀ (NRS); Rio Purus, Ilyutanaka, ♀ (NRS). *Acre*. Rio Purus, NW Sena Madureira, ♀ (MCZ); Abunã, ♀ (MCZ). *Rondônia*. Pôrto Velho, ♀ (MCZ). *Pará*. Rio Gurupi, 5♀ (AMNH); Forest Santarém, ♀ (BMNH); Canindé, 4♀ (AMNH); 50 km E Gurupi, ♂ (AMNH). *Bahia*. Uruça [?], ♀ (FZRS). BOLIVIA: *Prov. Beni*. Chacobo Indian village, Río Benicito, 2♀ (AMNH).

Micrathena schenkeli Mello-Leitão
Figures 480–489; Map 7

Micrathena schenkeli Mello-Leitão, 1939: 71, figs. 51–53, ♀. Female holotype from Paraguay (NMB), examined.

Micrathena gamma di Caporiacco, 1947: 26. Male type from Port Diamond [Great Diamond], British Guiana [Guyana] (MZUF), examined. 1948: 669, fig. 82, ♂. NEW SYNONYMY.

Micrathena browningi Chickering, 1960: 70, figs. 15–20, ♂. Male holotype from St. Diamond [Great Diamond], British Guiana [Guyana] (BMNH), examined. NEW SYNONYMY.

Micrathena gentilicia Chickering, 1964: 259, figs. 17–22, ♀. Female holotype from Trinidad, West Indies (MCZ), examined. NEW SYNONYMY.

Micrathena praeterita Chickering, 1964: 274, figs. 57–63, ♀. Female holotype from St. Augustine, Trinidad, Lesser Antilles (AMNH), examined. NEW SYNONYMY.

Synonymy. Chickering named the species three times: the male *M. browningi; M. gentilicia*, a female having the tip of the epigynum torn off; and *M. praeterita*, a virgin female with the epigynum undamaged. *Micrathena gamma* di Caporiacco is also a male.

Description. Female from Trinidad. Carapace dusky orange-brown. Sternum orange-yellow with some black pigment dots. Legs orange-brown. Dorsum of abdomen with white patches and some black areas; sides black; rows of white patches down sides; venter black with paired white patches. Carapace evenly arched, with shallow thoracic depression. Abdomen has six large, blunt spines (Figs. 480, 481). Total length, 4.5 mm. Carapace, 1.8 mm long, 1.2 mm wide. First femur, 1.4 mm; patella and tibia, 1.5 mm; metatarsus, 0.8 mm; tarsus, 0.5 mm. Second patella and tibia, 1.4 mm; third, 0.9 mm. Fourth femur, 1.7 mm; patella and tibia, 1.5 mm; metatarsus, 1.0 mm; tarsus, 0.6 mm.

Male from Minas Gerais. Carapace, sternum, legs brownish black. Abdomen with a median dorsal white mark and three pairs of white marks on the anterior edge; venter black. Carapace arched with a faint, indistinct longitudinal depression. Abdomen trapezoidal, posterior edge slightly curved (Fig. 487). Total length, 4.5 mm. Carapace, 2.2 mm long, 1.4 mm wide. First femur, 1.3 mm; patella and tibia, 1.5 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.9 mm. Fourth femur, 1.7 mm; patella and tibia, 1.4 mm; metatarsus, 0.9 mm; tarsus, 0.6 mm.

Variation. Females vary in total length from 4.5 to 6.2 mm, males from 4.5 to 5.0 mm. Some specimens, males and females, have almost no thoracic mark; in others this is present or is a very shallow groove (Fig. 487). The cymbium of the male palpus is widened and drawn out proximally (Figs. 488, 489), but in no two specimens does it have the same shape.

Note. Males and females were associated because they were both collected at Pedra Azul, Minas Gerais and Ondo Verde, São Paulo.

The wide semicircular lobe of the epigynum (Fig. 482) tears off when mating; most specimens lack this.

Diagnosis. The females can be separated from other species having an arched carapace by the six heavy abdominal spines (Fig. 481) and by having an epig-

ynum with a large semicircular lobe (Fig. 482). Usually this lobe is missing, and there is a divided depression (Figs. 485, 486).

The male differs from others having an indistinct thoracic depression by the proximally drawn out cymbium of the palpus (Figs. 488, 489) and the hook-shaped conductor (Fig. 488). The carapace of the male is less shiny than that of related species.

Natural History. Females were collected in Colombia in grass, brush along fence.

Distribution. Trinidad, Lesser Antilles, Colombia, Guyana to Paraguay (Map 7).

Records. LESSER ANTILLES: *Trinidad.* ♀ (N. Weber, MCZ); Balandra Bay, April 1922, 2♀ (Reynolds, MCZ); St. Augustine, 18 Sept. 1946, 15♀ (R. H. Montgomery, AMNH). *Curaçao.* ♀ (ZMK). VENEZUELA: *Est. Carabobo.* Bahia Patanemo, ♂ (MACN). *Distr. Fed.* Caracas, ♀ (NMW). GUYANA: Essequibo, 1895, ♀ (ZMK). SURINAME: Browns Berg, May 1984, ♀ (D. Smith, MCZ). COLOMBIA: *Meta.* Carimagua, 100 m el., Oct. 1973, 2♀ (W. Eberhard, MCZ). BRAZIL: *Terr. Amapá.* Serra do Navio, June 1966, ♀ (M. E. Galiano, MEG). *Est. Mato Grosso.* Barra do Tapirapé, Jan. 1966, ♀ (J. Malkin, MZSP). *Goiás.* Jaraguá, 12 June 1942, ♀ (F. Lane, MZSP). *Minas Gerais.* Pedra Azul, Dec. 1970, 3♀, 2♂ (F. M. Oliveira, AMNH). *Rio de Janeiro.* Duque de Caxias, Sept. 1961, 2♀ (M. Alvarenga, AMNH); Mangaratiba, Feb. 1976, ♂ (M. Alvarenga, AMNH). *São Paulo.* Onda Verde, Jan. 1946, ♀, ♂ (F. Lane, MZSP). PARAGUAY: ♀ (J. Viana, MZCN). ARGENTINA: *Prov. Misiones.* Santa María, Dec. 1947, 3♀ (J. Viana, MACN); Santa Ana, Nov.–Dec. 1958, ♀, ♂ (J. Viana, MACN); Monteagudo, Nov. 1956, ♀ (J. Viana, MACN).

Micrathena ucayali new species
Figures 490–497; Map 7

Type. Female holotype and four female paratypes from Río Ucayali between Atalaya and Pucallpa, Dept. Ucayali, Peru, 15 July to 4 August 1939 (W. F. Walker, Jr., MCZ). The specific name is a noun in apposition, named after the locality.

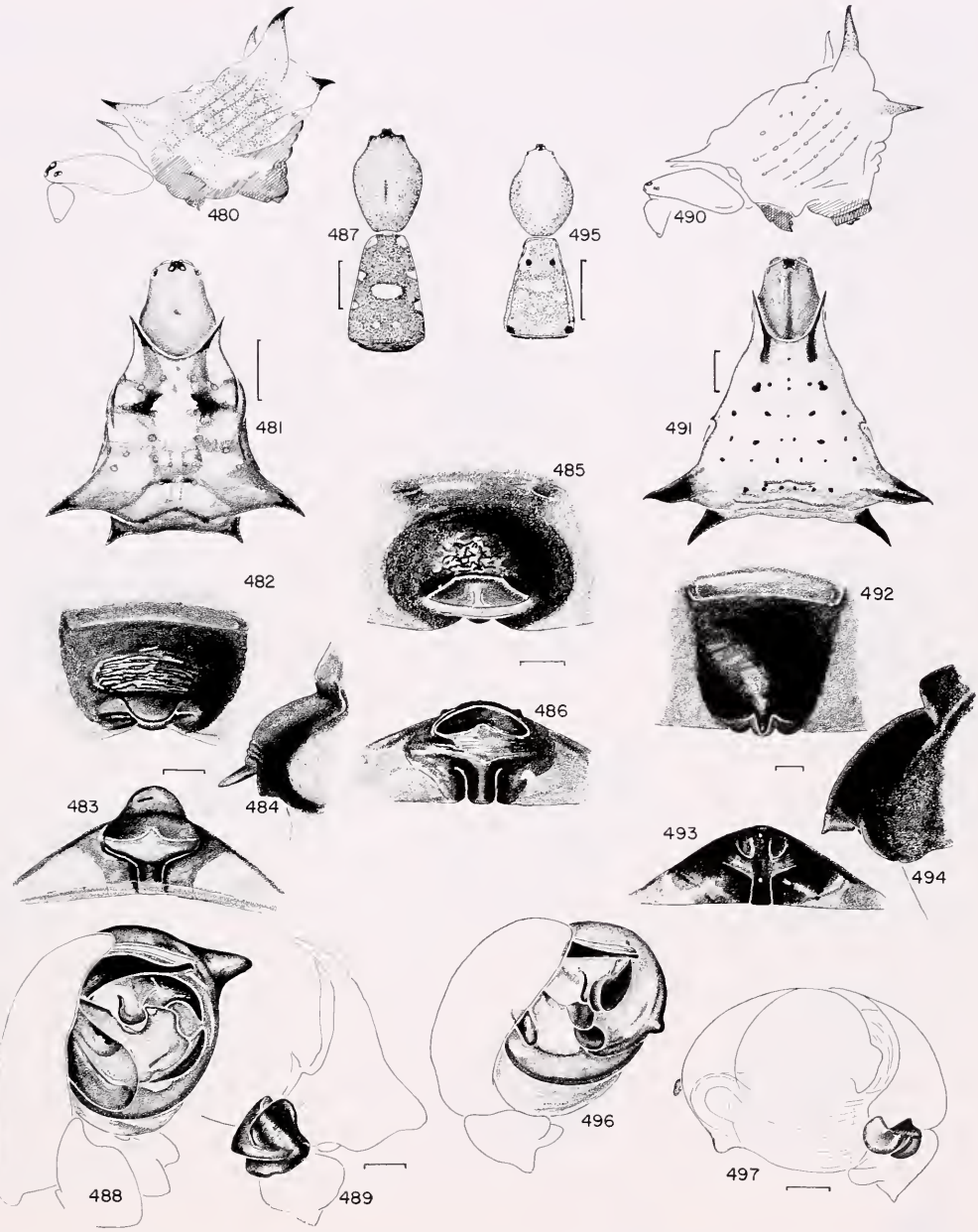
Description. Female. Carapace orange with median dusky line and sides of thorax dusky. Sternum orange underlain by white, with a black line along each side. Legs orange, dusky on anterior. Dorsum of abdomen with black spines, having white pigment on outside of anterior spines; sides grayish; venter black except for a pair of white marks behind genital groove; black all around spinnerets; some white on sides. Carapace arched, with a shallow indistinct thoracic depression. Posterior median eyes 1.5 diameters of others, which are subequal in size. Abdomen subtriangular with pair of spines overhanging carapace, a pair of large posterolateral spines, a pair of large posterior spines, and a small tooth on each side halfway between anterior and posterolateral spines (Figs. 490, 491). Total length, 6.0 mm. Carapace, 2.4 mm long, 1.9 mm wide. First femur, 2.2 mm; patella and tibia, 2.3 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm. Second patella and tibia, 2.0 mm; third, 1.5 mm. Fourth femur, 2.7 mm; patella and tibia, 2.2 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm.

Male. Carapace dark orange with thorax darker on sides and posterior. Sternum orange with white pigment spots. Legs orange. Dorsum of abdomen gray with a median white patch and four black patches, and some indistinct lighter areas. Venter orange-gray. Posterior median eyes twice diameter of anterior medians. No coxal hook. Abdomen trapezoidal (Fig. 495). Total length, 4.0 mm. Carapace, 1.9 mm long, 1.2 mm wide. First femur, 1.2 mm; patella and tibia, 1.2 mm; metatarsus, 0.7 mm; tarsus, 0.5 mm. Second patella and tibia, 1.0 mm; third, 0.7 mm. Fourth femur, 1.5 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 5.5 mm to 6.2 mm.

Note. Male and female were collected together on the upper Amazon.

Diagnosis. Micrathena ucayali differs from the similar *M. schenkeli* by having an additional pair of spines (Figs. 490,



Figures 480–489. *Micrathena schenkeli* Mello-Leitão. 480–486. Female. 480. Lateral. 481. Dorsal. 482, 485. Epigynum, ventral. 483, 486. Epigynum, posterior. 484. Epigynum, lateral. 485, 486. Lobe torn off. 487–489. Male. 487. Dorsal. 488. Left palpus, mesal. 489. Paracymbium, cymbium, lateral.

Figures 490–497. *Micrathena ucayali* n. sp. 490–494. Female. 490. Lateral. 491. Dorsal. 492. Epigynum, ventral. 493. Epigynum, posterior. 494. Epigynum, lateral. 495–497. Male. 495. Dorsal. 496. Palpus, mesal. 497. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 480, 481, 487, 490, 491, 495, 1.0 mm.

491), and by having a sharp tip on the epigynum at the most ventral point of the bulge (Fig. 492). Also, there is no notch above the tip in profile (Fig. 494), and in posterior view there is a depression on each side of the tip (Fig. 493). The male differs from others of the species group by having the sclerites of the median apophysis and conductor much closer to each other (Fig. 496) and by the shape of the paracymbium (Fig. 497).

Paratypes. PERU: *Dept. Loreto.* Pucallpa, 2 Oct. 1954, ♀ (E. I. Schlinger, E. S. Ross, CAS); Iquitos, Nov. 1961, juv. (J. Callan, AMNH); opposite Leticia, Colombia, 23 Feb. 1972, ♀ (CNC). *Ucayali.* Colonia Callaría, Río Callaría, 15 km from Ucayali, Oct. 1961, ♀ (B. Malkin, AMNH). BRAZIL: *Est. Amazonas.* São Paulo [São Paulo de Olivença], 3♀ (2494, MNHN); Benjamin Constant, 23 Dec. 1975, ♀ (A. Carvalho, FZRS); Alto Solimões, Dec. 1979, ♀, ♂ (A. Lise, FZRS).

Micrathena acuta (Walckenaer)
Figures 498–507; Map 7

Plectana acuta Walckenaer, 1841: 172. Female from Cayenne, French Guiana, lost.

Acrosoma acutum:—Keyserling, 1863: 71, pl. 2, fig. 4, ♀; 1892: 28, pl. 1, fig. 25, ♀.

Micrathena acuta:—Roewer, 1942: 953. Bonnet, 1957: 2860.

Pronous nigripes:—di Caporiacco, 1947: 25. Male paralectotype (not female lectotype, here designated) from Port Diamond [Great Diamond], British Guyana (MZUF), examined; 1948: 663, figs. 71, 72, ♂. NEW SYNONYMY.

Micrathena alpha di Caporiacco, 1947: 26. Immature holotype from Two Mouths, Essequibo, Guyana (MZUF), examined. NEW SYNONYMY.

Ildebaha inermis Schenkel, 1953: 28, fig. 25, ♂. Male holotype from El Pozón, Dpto. Acosta, Est. Falcón, Venezuela (NMB), examined. NEW SYNONYMY.

Synonymy. Walckenaer described the diagnostic six spines. Keyserling added that the sternum is highly arched.

Schenkel named the male *inermis*, and Caporiacco the immature *Micrathena alpha*.

Description. Female from Venezuela. Carapace orange-yellow, with darker sides and median line. Sternum brownish black. Coxae light orange, distal leg articles dusky orange. Dorsum of abdomen white with a black patch on lateral spines; insides of anterior spines and tips of posterior spines black (Figs. 498, 499); sides with a black patch; venter black; areas in midline without pigment; some white pigment patches on sides. Carapace arched, with indistinct, shallow thoracic depression. Sternum strongly arched (Fig. 510). Total length, 7.3 mm. Carapace, 2.7 mm long, 2.2 mm wide. First femur, 2.6 mm; patella and tibia, 2.7 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm. Second patella and tibia, 2.6 mm; third, 1.7 mm. Fourth femur, 3.3 mm; patella and tibia, 3.1 mm; metatarsus, 2.2 mm; tarsus, 0.8 mm.

Male from Colombia. Carapace, sternum, legs orange-brown. Dorsum of abdomen with four black spots and a median white patch (Fig. 503); venter black on dark orange, with some white pigment behind genital groove. Carapace oval, with indistinct thoracic depression. Eye proportions as in female. Sternum only slightly arched. First coxa without hook. First patella-tibia with some macrosetae ventrally; second patella-tibia thicker than first. Abdomen egg-shaped (Fig. 503). Total length, 4.0 mm. Carapace, 1.0 mm long, 1.1 mm wide. First femur, 1.3 mm; patella and tibia, 1.3 mm; metatarsus, 0.9

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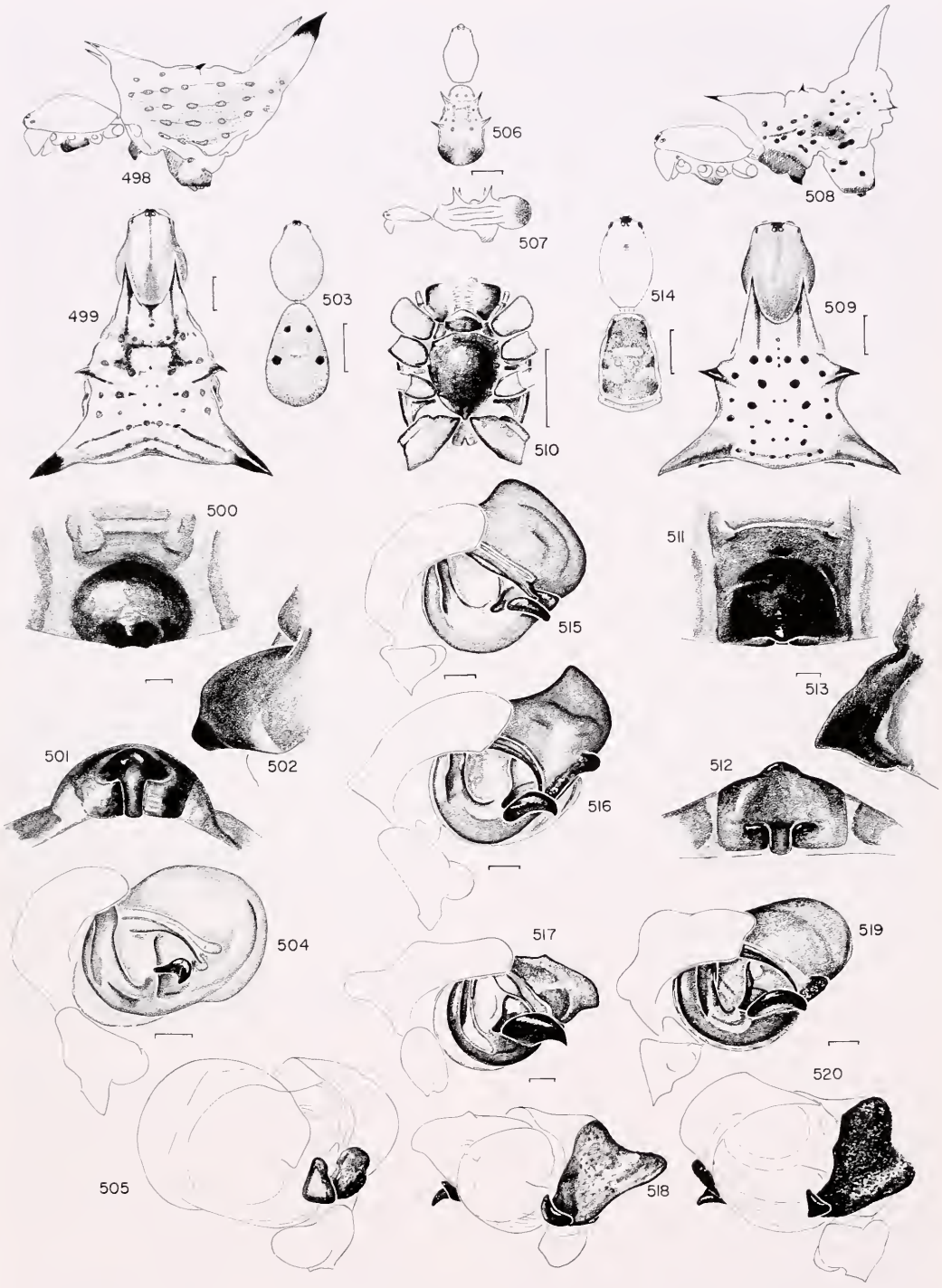
Figures 498–507. *Micrathena acuta* (Walckenaer). 498–502. Female. 498. Lateral. 499. Dorsal. 500. Epigynum, ventral. 501. Epigynum, posterior. 502. Epigynum, lateral. 503–505. Male. 503. Dorsal. 504. Left palpus, mesal. 505. Palpus, lateral. 506, 507. Immature (? male). 506. Dorsal. 507. Lateral.

Figures 508–520. *Micrathena flaveola* (C. L. Koch). 508–513. Female. 508. Lateral. 509. Dorsal. 510. Sternum, endites and coxae, 511. Epigynum, ventral. 512. Epigynum, posterior. 513. Epigynum, lateral. 514–520. Male. 514. Dorsal. 515–517, 519. Palpus, mesal. 518, 520. Palpus, lateral. 515. (Prov. Misiones, Argentina). 516. (Manaus, Brazil). 517, 518. (Tingo María, Peru). 519, 520. (Costa Rica).

Scale lines. 0.1 mm, except Figures 498, 499, 503, 506–510, 514, 1.0 mm.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mm; tarsus, 0.5 mm. Second patella and tibia, 1.4 mm; third, 0.6 mm. Fourth femur, 1.4 mm; patella and tibia, 1.4 mm; metatarsus, 1.1 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 5.3 to 7.3 mm, males from 3.9 to 4.0 mm. Females may be much darker in color, with a pattern resembling that of *M. triangularispinosa*. Some females have a tubercle posteriorly on the abdomen below the posterolateral spines. The bulbous portion of the male palpal bulb varies slightly in outline.

Note. Male and female were collected together in Colombia and northern Brazil.

Diagnosis. Like *M. flaveola*, females have a swollen sternum (Fig. 510). Females differ from *M. flaveola* by having only six spines, lacking the fourth pair of spines on the posterior of the abdomen (Figs. 498, 499). In ventral view there is a faint transverse groove on the swelling of the epigynum (Fig. 502); in posterior view the parallel, paraxial slits appear much longer (Fig. 501) than in *M. flaveola*.

Males, like those of *M. flaveola*, have the bulb distally swollen (Figs. 504, 505), but differ by having the sculptured area of the cymbium facing the paracymbium small (Fig. 505).

Distribution. Trinidad, Lesser Antilles, Peru, Brazil (Map 7).

Records. LESSER ANTILLES: *Trinidad.* ♀ (MCZ). VENEZUELA: *Est. Carabobo.* San Esteban, Jan. 1940, 2♀ (P. Andruze, CUC), Aug. 1975, ♀ (Martinez, MACN). *Distr. Fed.* Caracas, ♀ (NMW). *Monagas.* Caripito, March, April 1942, 3♀ (W. Beebe, AMNH). GUYANA: Canister Fall, 3 July 1923, ♀ (G. E. Bodlin, BMNH). FRENCH GUIANA: St. Laurent de Maroni, ♂ (K. Jelski, PAN). COLOMBIA: *Dept. Meta.* 15 km SW Puerto Lopez, 1978, 3♀, ♂ (W. Eberhard, MCZ); Villavicencio, 19 July 1938, ♀ (H. Dybas, AMNH), 2♀ (Fasel, NMW). *Putumayo.* Buena Vista, 23–29 July 1972, ♀ (W. Eberhard, MCZ). ECUADOR: *Prov. Napo.* R. F. Cuyabeno, 6 March 1983, 15 Feb. 1984, 7 ♀ (L. Avilés, MECN). PERU: *Dept. San Martín.* 20 km NE of Moyobomba, 1,600 m, Aug. 1947, ♀ (F. Woytkowski, EPC). BRAZIL: *Terr. Amapá.* Serra de Navio, June 1966, ♀, ♂ (M. E. Galiano, MEG). *Est. Pará.* Belém, Aug. 1971, 2♀ (M. E. Galiano, MEG); Rio Gurupi, 1963, ♀ (B. Malkin, MZSP). *Amazonas.* Rio Negro, Umarituba, 20 April 1924, ♀ (A. Roman, NRS). *Rondônia.* Vila Murtinho, 3 March 1922, ♀ (J. H. Williamson, MCZ). *Bahia.* Uruçuca, 26 Nov. 1977, ♀ (J. S. Santos, FZRS). *Goiás.* Jataí, Oct. 1962, ♀ (Exp. Dept. Zool, MZSP). *Mato Grosso.* Barra de Tapirapé, July–Aug. 1962, Jan. 1963, 2♀ (B. Malkin, AMNH). *Rio de Janeiro.* Teresópolis, ♀ (E. Reimoser, MCZ). ARGENTINA; *Prov. Misiones.* Punto Aguirre, 1943, ♀ (J. Viana, MACN).

Micrathena flaveola (C. L. Koch)
Figures 8, 508–520; Map 7

Acrosoma aculeatum:—C. L. Koch, 1836: 58, fig. 211, ♀. Misidentification, not *M. aculeata* Fabricius.

Acrosoma flaveola C. L. Koch, 1839: 126, fig. 522, ♀. Female from Brazil (ZSM), destroyed.

Plectana gladiola Walckenaer, 1841: 182. New name for *A. aculeatum* C. L. Koch. NEW SYNONYMY.

Acrosoma vitiosum O. P.-Cambridge, 1890: 63, pl. 8, fig. 14, ♂. Two male syntypes from Bugaba, Panama (BMNH), examined. Keyserling, 1892: 10, pl. 1, fig. 7, ♂. NEW SYNONYMY.

Acrosoma fericula O. P.-Cambridge, 1890: 64, pl. 8, fig. 13. Juvenile female lectotype here designated from Bugaba, Panama (BMNH), examined. NEW SYNONYMY.

Acrosoma flaveolum:—Keyserling, 1892: 8, pl. 1, fig. 5, ♀.

Ildibaha albomaculata Keyserling, 1892: pl. 2, fig. 29. Immature holotype from Blumenau [Est. Santa Catarina, Brazil] (BMNH), lost. NEW SYNONYMY.

Micrathena vitiosa:—F. P.-Cambridge, 1904: 532, pl. 50, fig. 11, ♂. Roewer, 1942: 966. Bonnet, 1957: 2881. Chickering, 1961: 466, figs. 206–210, ♂.

Micrathena gladiola:—F. P.-Cambridge, 1904: 537. Reimoser, 1917: 145. Roewer, 1942: 958. Bonnet, 1957: 2868. Chickering, 1961: 419, figs. 67–71, ♀.

Micrathena fericula:—F. P.-Cambridge, 1904: 539.

Ildibaha fericula:—Mello-Leitão, 1932: 94. Roewer, 1942: 952. Bonnet, 1957: 2296.

Synonymy. C. L. Koch described the arched carapace, the arched, "egg-shaped"

sternum, and the eight spines for *M. flaveola*. *Acrosoma aculeatum* of C. L. Koch, a misidentification renamed *Plectana gladiola* by Walckenaer, appears to be the same. *Acrosoma vitiosum* is the male. *Acrosoma fericula* is an immature, apparently collected with *A. vitiosum*. *Ildibaha albomaculata* is an immature of this or of a related species in this group.

The illustrations were made from a male and female from Costa Rica.

Description. Female from Costa Rica. Carapace orange-brown, darker on sides. Sternum dark brown. Legs dark orange. Dorsum of abdomen white with a black line on inside of anterior spines; lateral spines black; large posterior spines orange; sides with black patches; venter light orange with brown sclerotized spots. Carapace high, without mark except for indistinct thoracic dent. Sternum convex, bulging (Fig. 510). Abdomen with four pairs of spines (Figs. 508, 509). Total length, 6.5 mm. Carapace, 2.8 mm long, 2.0 mm wide. First femur, 2.4 mm; patella and tibia, 2.4 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm. Second patella and tibia, 2.3 mm; third, 1.6 mm. Fourth femur, 3.2 mm; patella and tibia, 2.6 mm; metatarsus, 1.9 mm; tarsus, 0.9 mm.

Male from Costa Rica. Carapace, sternum dark brown. Legs grayish brown. Dorsum of abdomen with anterior transverse white line and median white patch on brown; six black patches. Venter with brown sclerotized areas, soft areas black. First coxa without hook. First and second femora with some short macrosetae ventrally and proximally. Abdomen trapezoidal, narrow anteriorly, rounded behind, slightly lobed on sides (Fig. 514). Total length, 4.4 mm. Carapace, 2.0 mm long, 1.2 mm wide. First femur, 1.5 mm; patella and tibia, 1.4 mm; metatarsus, 0.9 mm; tarsus, 0.6 mm. Second patella and tibia, 1.3 mm; third, 0.9 mm. Fourth femur, 1.9 mm; patella and tibia, 1.5 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm.

Variation. Females vary in total length from 6.3 to 7.2 mm, males from 4.0 to 4.8 mm. A thoracic dent may sometimes be visible. There may be some sculpturing posteriorly on the epigynum. The swollen tegulum of the male palpus varies in outline among individuals (Figs. 515–519).

Note. Living specimens are yellow, with large spines purplish. Males and females were associated because they belong to the same species group, lacking a thoracic indentation. Males and females have been collected from Costa Rica to Argentina. Penultimate immatures have the sternum black and only slightly convex; the epigynal area is sclerotized and spherical.

Diagnosis. Females of this species differ from all others, except *M. acuta*, by having a swollen sternum (Fig. 510). They differ from *acuta* by having eight spines rather than six, a small fourth pair behind the large posterolaterals (Figs. 508, 509). In addition, the shape of the epigynum differs: there is a faint arch-shaped impression on the swelling (Fig. 513), and in posterior view the paraxial parallel slits are quite short, ending some distance from the tip (Fig. 512). The male differs from *M. acuta* by having a large sculptured area on the cymbium facing the paracymbium (Figs. 518, 520).

Distribution. Costa Rica to northern Argentina (Map 7).

Records. COSTA RICA: *Prov. Limón.* Hamburg Farm, ♀ (MCZ); Lalola, ♀ (MCZ). *Cartago.* Turrialba, 2♀ (AMNH). *Heredia.* La Selva, Puerto Viejo, ♂ (MCZ). PANAMA: *Prov. Panamá.* Madden Dam, ♀ (AMNH). VENEZUELA: *Est. Monagas.* Caripito, ♀ (AMNH). *Carabobo.* Bahia Patanemo, 2♀ (MACN). *Dist. Fed.* Caracas, ♀ (NMW). GUYANA: *Bartica Distr.* Kartabo, 2♀, ♂ (AMNH); Kaietur, ♀ (AMNH). FRENCH GUIANA: Cayenne, 3♀ (PAN); St. Laurent de Maroni, ♀ (AMNH). COLOMBIA: *Dept. Meta.* Villavicencio, ♀♀ (AMNH, NMW); Caño Grande, ♀ (AMNH). *Santander.* Río Suárez, 800–1,000 m, 2♀ (AMNH). *Coquéta.* Río Orteguaza, ♀ (AMNH). ECUADOR: *Prov. Napo.* Tarapuy, 2♀ (MECN). PERU: *Dept. Loreto.* Loreto, 3♀ (MCZ); Río

Bambo, Alto Tapiche, ♀ (MZSP). *San Martín.* Saposoa, Río Huallaga, 2♀ (EPC). *Huánuco.* Tingo María, 4♀ (AMNH); Monsón Valley, Tingo María, ♀, ♂ (CAS); 67 km E Tingo María, ♀ (CAS). *Ucayali.* Mishana, ♀ (MPM). *Huancavelica.* Valle Chanchamayo, 2♀ (EPC). BRAZIL: *Est. Amazonas.* Tefé, ♀ (MCZ); Manaus, ♂ (MEG); Rio Autas, Capiranga, ♀ (NRS); Taracuá, 2♀ (NRS). *Pará.* Belém, ♀ (AMNH); Canindé, Rio Gurupi, ♀ (AMNH). *Bahia.* Camacari, ♀ (FZRS); Salvador, ♀ (ZMK). *Espírito Santo.* Colatina, 3♀ (MNRJ); Rio São José, ♀ (MZSP). *Rio de Janeiro.* Rio de Janeiro, ♀ (ZMK). Teresópolis, ♀ (E. Reimoser, MCZ). *São Paulo.* Bertioga, ♀ (MZSP). *Santa Catarina.* Corupá, ♀ (AMNH); 3♀ (MZSP). BOLIVIA: *Prov. Beni.* Chacobo Village, Río Benicito, ♀ (AMNH). *Cochabamba.* Gral. Roman, 2♀ (MULP); Río Chipiri, ♀ (ZSM). ARGENTINA: *Prov. Misiones.* Eldorado, 5♀, 2♂ (AMNH, MULP); Montecarlo, 4♀ (AMNH); Parque Nac. Iguazú, ♂ (MEG); Punto Rieo, ♀ (MACN); Punto 17 de Octubre, ♀, ♂ (MACN); Puerto Aguippe, ♀ (MULP); San Ignacio, ♀ (MULP).

Micrathena ornata Mello-Leitão
Figures 521–524; Map 7

Micrathena ornata Mello-Leitão, 1932: 86, fig. 4, ♀. Female holotype from Niterói, Brazil (MNRJ), examined.

Type. The abdomen of the type is shrivelled and transversely shrunken. It seems to have been dried at one time. It does not look much like figure 4 of Mello-Leitão, but the description fits this species. It was examined some time before this study was started.

Description. Female. Carapace, sternum, legs orange-brown. Dorsum of abdomen white with sclerotized areas orange-brown. Sides with white pigment streaks between grooves. Venter with white transverse bars posterior to spinnerets. Carapace completely smooth, high, rounded posteriorly, with a small indistinct circular thoracic depression (Fig. 522). Total length, 6.0 mm. Carapace, 2.0 mm long, 1.8 mm wide. First patella and tibia, 2.2 mm; second, 1.8 mm; third, 1.2 mm. Fourth femur, 2.3 mm.

Diagnosis. This species differs from others of the *M. triangularispinosa* group by having twelve abdominal spines (Figs. 521, 522) and by the structure of the epigynum (Figs. 523, 524).

Note. No other specimens have been found.

The *lepidoptera* Group

Females from this group are distinguished by having compound spines on the sides of the abdomen (Figs. 526, 535) and by having a small, light colored median scape behind the top of the bulge of the epigynum (Figs. 527, 536). The carapace, unlike that of the *M. triangularispinosa* group, has a thoracic depression and dimples. The male lacks a coxal hook and has a two-part median apophysis and a large paracymbium which projects laterally (Figs. 531–533, 540–542).

The carapace of the female has a high thorax, and a narrow rim and a distinct thoracic depression (Figs. 525, 526, 534,

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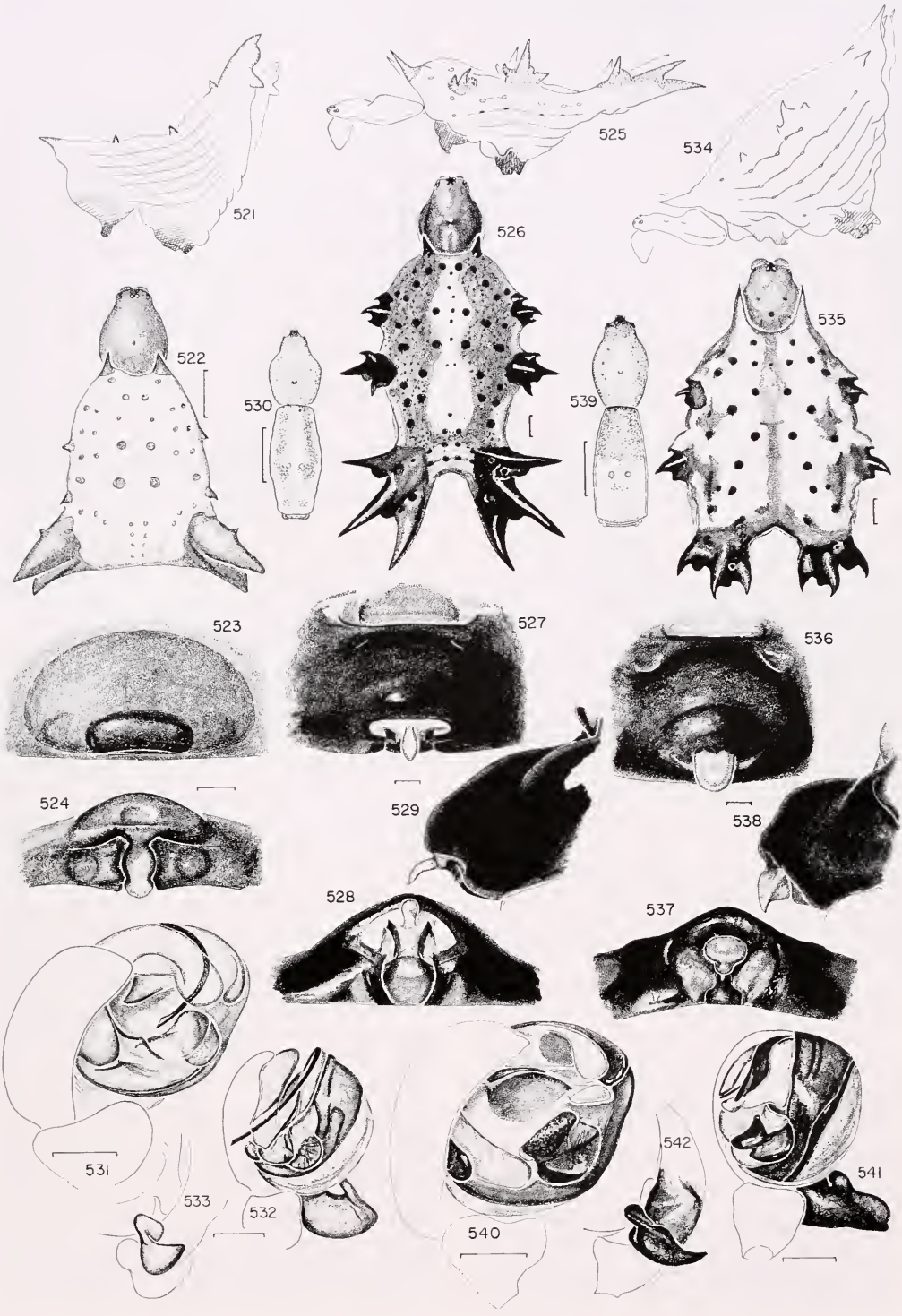
Figures 521–524. *Micrathena ornata* Mello-Leitão, female. 521. Abdomen, lateral. 522. Dorsal. 523. Epigynum, ventral. 524. Epigynum, posterior.

Figures 525–533. *Micrathena lepidoptera* Mello-Leitão. 525–529. Female. 525. Lateral. 526. Dorsal. 527. Epigynum, ventral. 528. Epigynum, posterior. 529. Epigynum, lateral. 530–533. Male. 530. Dorsal. 531. Left palpus, mesal. 532. Palpus, ventral. 533. Paracymbium, lateral.

Figures 534–542. *Micrathena decorata* Chickering. 534–538. Female. 534. Lateral. 535. Dorsal. 536. Epigynum, ventral. 537. Epigynum, posterior. 538. Epigynum, lateral. 539–542. Male. 539. Dorsal. 540. Palpus, mesal. 541. Palpus, ventral. 542. Paracymbium, lateral.

Scale lines. 0.1 mm, except Figures 521, 522, 525, 526, 530, 534, 535, 539, 1.0 mm.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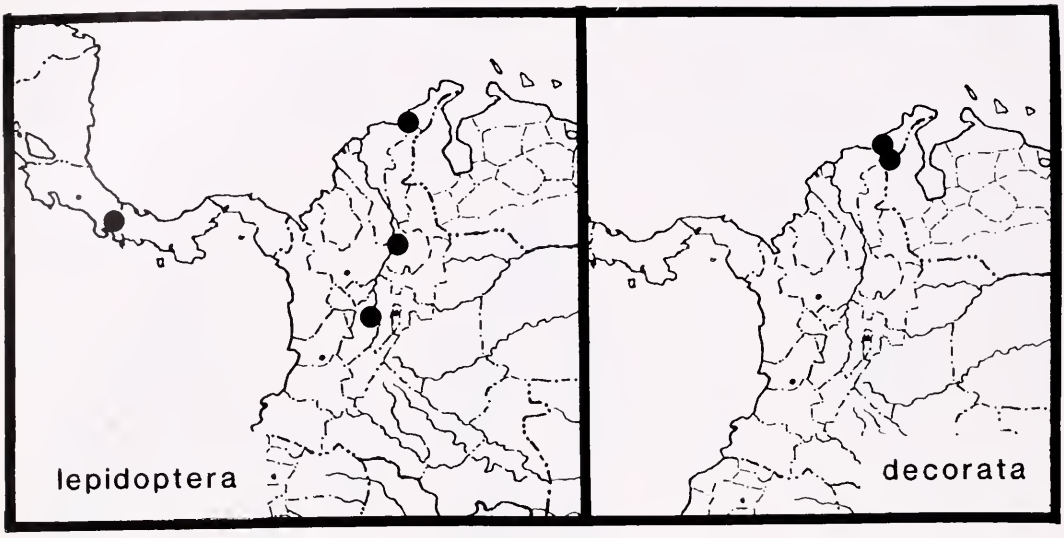


Map 8. Distribution of *Micrathena* species of the *lepidoptera* group.

535). The abdomen not only has six compound spines, spines overhanging the carapace, but also a blunt spine on the venter, on each side of the spinnerets (Figs. 525, 534). The carapace of the male is relatively flat with thoracic mark, the abdomen rectangular, longer than wide, slightly convex on the sides, with two pairs of minute tubercles on posterior folds (Figs. 530, 539). The genitalia of the two species are much like those of the *triangularispinosa* group.

The females of the two species are easiest to separate by the epigynum and dorsal color markings, the males by the length of the embolus and shape of the paracymbium.

The species are found from Costa Rica to Colombia (Map 8).

KEY TO THE *LEPIDOPTERA* GROUP

1. Female with epigynal scape as wide as long and almost as thick (Figs. 536, 538); abdomen with a dark median longitudinal band (Fig. 535); male with pointed paracymbium (Fig. 542) and short embolus (Fig. 540); northern Colombia, Map 8 ..... *decorata*
– Epigynal scape more than twice as long as wide (Figs. 527, 529); abdomen with a light median longitudinal band (Fig. 526); male with blunt paracymbium (Fig. 533) and long embolus (Fig. 531); Costa Rica to Colombia, Map 8 ..... *lepidoptera*

Micrathena lepidoptera Mello-Leitão
Plate 2; Figures 525–533; Map 8

Micrathena lepidoptera Mello-Leitão, 1941: 266, fig. 3, ♀. Female holotype from La Petrolera, Catatumbo [4°02'N, 75°07'W, Dept. Tolima, Colombia] (MNRJ), lost.

Type. Mello-Leitão's illustration of the female abdomen confirms the name of this species.

Description. Female from Costa Rica. Carapace dark brown with light rim. Sternum dark brown. Coxae and distal leg articles slightly lighter grayish brown. Dorsum of abdomen with blackish spines, sides of dorsum black, middle yellow-orange; venter black with an orange patch on each side of epigastric area and one on each side of spinnerets, which enclose a blunt ventral spine. Carapace with high thorax and distinct median thoracic depression, three grooves, no dimples. Abdomen with three pairs of trifid spines (Fig. 526) and a pair of blunt spines on the venter on either side of spinnerets (Fig. 525). Total length, 13.2 mm. Carapace, 4.0 mm long, 3.2 mm wide. First femur, 4.2 mm; pa-

tella and tibia, 4.2 mm; metatarsus, 2.6 mm; tarsus, 1.1 mm. Second patella and tibia, 3.6 mm; third, 2.3 mm. Fourth femur, 4.6 mm; patella and tibia, 3.7 mm; metatarsus, 2.9 mm; tarsus, 1.1 mm.

Male. Carapace dark brown. Sternum black. Coxae and distal leg articles yellow-white. Dorsum of abdomen yellow-white with black marks (Fig. 530); venter black. Carapace with distinct thoracic depression, without dimples. First coxa without hook. Fourth legs slightly shorter than first. Sides of abdomen almost parallel (Fig. 530). Total length, 3.3 mm. Carapace, 1.3 mm long, 0.9 mm wide. First femur, 1.6 mm; patella and tibia, 1.4 mm; metatarsus, 0.8 mm; tarsus, 0.4 mm. Second patella and tibia, 1.1 mm; third, 0.6 mm. Fourth femur, 1.3 mm; patella and tibia, 1.0 mm; metatarsus, 0.8 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 12.6 to 13.2 mm.

Note. The male was not collected with the female. It is similar to the presumed male of *M. decorata*. Also, the collector, John Kochalka, had marked it as belonging to the females he collected from nearby.

Diagnosis. The narrow scape of the epigynum (Fig. 527) and the median light dorsal area of the abdomen (Fig. 526) separate this species from *M. decorata*. Differences in shape of the paracymbium (Fig. 533), median apophysis and the threadlike embolus (Fig. 531) separate the male from that of *M. decorata*.

Distribution. Costa Rica to Colombia (Map 8).

Records. COSTA RICA: *Prov. Puntarenas.* San Vito, Las Cruces, 6 March 1979, 20 Aug. 1979, 2♀ (J. Coddington, MCZ). COLOMBIA: *Dept. Santander.* Río Opón, 1,000 m, Jan. 1947, ♀ (L. Richter, AMNH). *Boyacá.* Río Dpan [?], Nov.–Dec. 1945, 2♀ (AMNH). *Magdalena.* San Pedro, Sierra Nevada de Santa Marta, 1,000 m, 8 Feb. 1974, ♀ (J. Kochalka, JAK); above Minca Valley, Sierra Nevada de Santa Marta, 880 m, 24 Feb. 1974, ♂ (J. Kochalka, JAK).

Micrathena decorata Chickering
Figures 534–542; Map 8

Micrathena decorata Chickering, 1960c: 73, figs. 29–32, ♀. Female holotype from New Granada [Spanish colony of Colombia and Panama] (BMNH), examined.

Description. Female. Carapace blackish brown. Sternum, legs black. Dorsum of abdomen with black spines and median dark longitudinal line on yellow-white (Fig. 535); sides, venter with white patches. Carapace with two pairs of dimples and median thoracic depression; rim narrow in dorsal view, thorax high. Abdomen with a simple pair of spines overhanging carapace, two pairs of trifid spines on sides, a pair of posterolateral trifid spines (Fig. 535), and a blunt spine on each side of spinnerets (Fig. 534). Total length, 11.2 mm. Carapace, 3.8 mm long, 3.2 mm wide. First femur, 3.9 mm; patella and tibia 3.9 mm; metatarsus, 2.4 mm; tarsus, 1.0 mm. Second patella and tibia, 3.5 mm; third, 2.2 mm. Fourth femur, 4.4 mm; patella and tibia, 3.7 mm; metatarsus, 2.7 mm; tarsus, 1.0 mm.

Male. Carapace black with some brown in middle of thorax. Sternum black. Coxae yellowish white, other leg articles brownish black, distal articles darkest. Dorsum of abdomen with anterior half black, a median dusky mark, and posterior blackish on yellow-white; venter gray. Carapace with three pairs of dimples and a distinct thoracic depression. First coxae without hook. The femur of the first leg is longer than fourth. Sides of abdomen almost parallel (Fig. 539). Total length, 3.7 mm. Carapace, 1.7 mm long, 1.0 mm wide. First femur, 1.7 mm; patella and tibia, 1.6 mm; metatarsus, 1.1 mm; tarsus, 0.5 mm. Second patella and tibia, 1.3 mm; third, 0.7 mm. Fourth femur, 1.4 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 8.2 to 11.2 mm.

Note. The male was collected with females of *M. decorata*, *M. lucasi* and *M.*

sexspinosa at Finca San José, 8 km SE of Socorpa Mission, Colombia.

Diagnosis. The wide scape of the epigynum (Fig. 536) separates females of this species from *M. lepidoptera*. Males are distinguished by the pointed paracymbium (Fig. 542) and the short embolus (Figs. 540, 541).

Distribution. Northeastern Colombia (Map 8).

Records. COLOMBIA: *Dept. Magdalena.* Sierra Nevada de Santa Marta, Cerro Lagila, 1,400 m, 30 April 1975, 3♀ (J. Kochalka, JAK). *Cesar.* Socorpa Mission, 1,350 m, 2 Aug. 1968, ♀, 1,500–1,600 m, 16–17 Aug. 1968, ♀ (B. Malkin, AMNH); 8 km SE Socorpa Mission, 1,450–1,500 m, near San José village, 27–31 July 1968, 2♀, ♂ (B. Malkin, AMNH).

The *schreibersi* Group

Females are characterized by having a pair of keels at the posterior margin of the epigynum (Figs. 554, 559, 568, 576; absent in *M. spitzi,* Fig. 546). Males are distinguished by having their abdomen constricted in the middle, violin-shaped (Figs. 548, 561, 570, 579), seemingly lacking a terminal apophysis in the palpus and having a complex median apophysis comprised of several parts (Figs. 549, 562, 571, 580).

The carapace of the female has a wide rim, a thoracic depression (Figs. 552, 565, 574), and a pair of dimples. The thorax is relatively low, widest anteriorly. The rim and dimples are absent in *M. spitzi.* The abdomen is armed with ten spines, the fourth pair the longest (Figs. 565, 574), except *M. embira* which has 14 spines (Fig. 552). Except for *M. spitzi* (Fig. 544), a pair of short spines overhangs the carapace. The epigynum has a median squarish overhanging piece at the tip of the bulge, wider than long, and attached anteriorly (Figs. 553, 567, 575). Males have a shiny carapace with an indistinct thoracic depression; *M. schreibersi* and *M. balzapamba* have a pair of dimples. Males lack a coxal hook and the groove on the second femur.

It is uncertain whether *M. embira* belongs to the group, since the male is unknown; *M. spitzi* probably does.

Diagnostic features for species are the position of the spines on the abdomen of females and the epigynum; for males, the structure of the palpus.

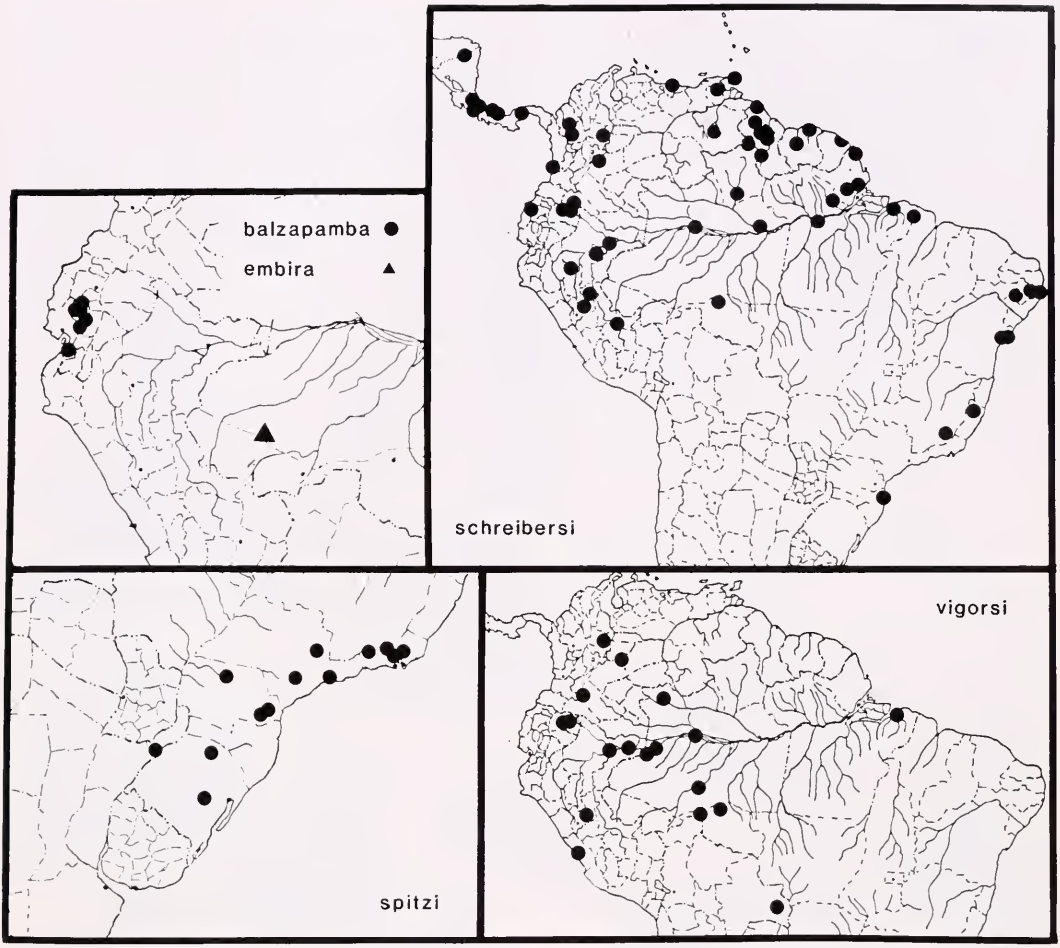
KEY TO SPECIES OF THE *SCHREIBERSI* GROUP

1. Females abdomen with 14 spines, the fifth pair large and bent forward (Figs. 551, 552); epigynum with a median lobe on anterior of bulge (Figs. 553–555); male unknown; upper Amazon, Map 9 ..... *embira*
– Female abdomen with 10 spines or humps (Figs. 544, 566); epigynum otherwise 2
2(1) Female abdomen with pointed humps and no spines anterior (Figs. 543, 544); male with abdomen constricted near posterior end (Fig. 548) and palpal median apophysis as in Figure 549; southeastern Brazil, Map 9 ..... *spitzi*
– Female abdomen with large spines, short spines anteriorly overhanging carapace (Figs. 557, 565, 574); male with abdomen constricted closer to anterior end (Figs. 561, 570, 579) 3
3(2) Epigynum with anterior, dark, sclerotized lobe (Figs. 567, 575); male palpus with base of median apophysis bearing a sclerite (Figs. 571, 580) 4
– Epigynum with an anterior transverse ridge (Figs. 558–560); male palpus without folded sclerite on base of median apophysis (Fig. 562); Western Ecuador, Map 9 ..... *balzapamba*
4(3) Females with area between second and third spine pair longer than wide (Fig. 574); males with a prong on median apophysis of palpus (Fig. 580); Amazon area, Map 9 ..... *vigorsi*
– Female with area between second and third spine pair wider than long (Fig. 565); males with median apophysis with rim pointing toward cymbium of embolus (Fig. 571); Nicaragua to southeastern Brazil, Map 9 ..... *schreibersi*

Micrathena spitzi Mello-Leitão
Figures 543–550; Map 9

Micrathena spitzi Mello-Leitão, 1932: 79, fig. 2, ♀. Female holotype from Alto da Serra, Est. São Paulo, Brazil (MNRJ), examined.

Ildibaha misionesica Mello-Leitão, 1945a: 238, figs. 12–13, ♀. Juvenile (penultimate female) holotype



Map 9. Distribution of *Micrathena* species of the *schreibersi* group.

from Pindapoy, Misiones Province, Argentina (MULP), examined. NEW SYNONYMY.

Ildibaha acanthomasta Mello-Leitão, 1945b: 264, figs. 4, 6, ♀. Female holotype from Bariguí, Paraná, Brazil in the Museu Paranaense, not available. NEW SYNONYMY.

Synonymy. Mello-Leitão named this species three times. The abdomen of the *M. spitzi* type specimen is shrivelled. *Ildibaha acanthomasta* was recognized from the illustrations.

Description. Female. Carapace rich brown. Sternum orange to dark brown. Legs light brown, banded darker; distal articles lighter. Dorsum of abdomen *Cyclosa*-like with black and white paired and median marks; sides black with two dorsoventral white bands, one anterior, one about the middle; venter black (Fig. 544). Carapace widest in anterior half, with an indistinct median thoracic mark and a slight depression on each side posteriorly (Fig. 544). Femora with rows of indistinct humps on venter. Abdomen soft, *Cyclosa*-like, without sclerotized plates on sides, five pairs of humps, each tipped by a tiny spine, and sclerotized ring around spinnerets (Figs. 543, 544). Total length, 12.5

mm. Carapace, 4.0 mm long, 2.4 mm wide. First femur, 2.9 mm; patella and tibia, 2.9 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm. Second patella and tibia, 2.7 mm; third, 1.9 mm. Fourth femur, 3.7 mm; patella and tibia, 3.5 mm; metatarsus, 2.3 mm; tarsus, 0.9 mm.

Male. Carapace, sternum dark brown. Legs orange, articles darker on anterior and posterior. Dorsum of abdomen black with some paired white spots (Fig. 548); venter black. No coxal hook. First and second femora have pairs of indistinct humps. Abdomen with several constrictions, like female (Fig. 548). Total length, 6.7 mm. Carapace, 3.2 mm long, 1.9 mm wide. First femur, 1.9 mm; patella and tibia, 1.9 mm; metatarsus, 1.3 mm; tarsus, 0.7 mm. Second patella and tibia, 1.8 mm; third, 1.1 mm. Fourth femur, 2.4 mm; patella and tibia, 2.1 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm.

Variation. Females vary in total length from 10.2 to 14.1 mm. The shape of the projecting epigynum is slightly variable.

Note. The similarity of male and female suggests that they belong together.

Diagnosis. Micrathena spitzi differs from all other *Micrathena* by its *Cyclosa*-like appearance: abdomen two to three times as long as wide, with ten humps (Figs. 543, 544), and the epigynum which has the bulge indented on each side anteriorly (Figs. 545, 547). The male is separated from others having the abdomen constricted posteriorly (Fig. 548) and by the distinct median apophysis having one tooth (Fig. 549).

Natural History. Two specimens were collected in forest near São Paulo.

Distribution. Southeastern Brazil (Map 9).

Records. BRAZIL: *Est. Rio de Janeiro.* Teresópolis, 11 March 1946, 3♀ (H. Sick, AMNH); Petrópolis, 2♀ (Arlé, MNRJ); Rezende, ♀ (Arlé, MZSP). *São Paulo.* São Paulo, 10 April 1965, 2♀ (H. Levi, MCZ), 3♀ (P. Biasi, MZSP); Pirassununga, ♀ (Schubart, MZSP); Aqua Tunda, 16 March 1961, ♂ (H. M. Canter, MZSP). *Paraná.* Rolândia, 1947, 4♀ (A. Maller, AMNH); Cavinna, 1947, 6♀ (A. Maller, AMNH). *Rio Grande do Sul.* Itaúba, Arroio do Tigre, 18 April 1978, 4♀ (A. Lise, FZRS); Cachoeira do Sul, 3 July 1977, ♀ (A. Witeck, FZRS).

Micrathena embira new species
Figures 551–555; Map 9

Holotype. Female from mouth of Rio Embira, Rio Jurura, N. Amazonia [sic, western Amazonia], Brazil, in poor condition, having oviposited and having lost most legs (AMNH). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace blackish brown, rim light. Sternum, legs brown. Abdomen leathery dark brown underlain with some white pigment. Carapace with one pair of anterior dimples and distinct thoracic depression. Abdomen with fourteen spines, the fifth pair, the posterolaterals largest (Figs. 551, 552). Total length, 8.9 mm. Carapace, 3.0 mm long, 2.2 mm wide. First femur, 3.0 mm. Fourth femur, 3.7 mm; patella and tibia, 3.0 mm; metatarsus, 2.0 mm.

Diagnosis. The fourteen spines of the abdomen (Figs. 551, 552) and the epigynum, with its small projecting lobe on the anterior face of the globular bulge (Figs. 553–555), separate *M. embira* from others of the *schreibersi* group.

Micrathena balzapamba new species
Figures 556–563; Map 9

Holotype. Female from Balzapamba, Bolívar Prov., Ecuador, 700 m el., June 1938 (W. Clarke-MacIntyre, AMNH). The species is named after the

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Figures 543–550. *Micrathena spitzi* Mello-Leitão. 543–547. Female. 543. Lateral. 544. Dorsal. 545. Epigynum, ventral. 546. Epigynum, posterior. 547. Epigynum, lateral. 548–550. Male. 548. Dorsal. 549. Left palpus, mesal. 550. Palpus, lateral.

Figures 551–555. *Micrathena embira* n. sp., female. 551. Lateral. 552. Dorsal. 553. Epigynum, ventral. 554. Epigynum, posterior. 555. Epigynum, lateral.

Figures 556–563. *Micrathena balzapamba* n. sp. 556–560. Female. 556. Lateral. 557. Dorsal. 558. Epigynum, ventral. 559. Epigynum, posterior. 560. Epigynum, lateral. 561–563. Male. 561. Dorsal. 562. Palpus, mesal. 563. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 543, 544, 548, 551, 552, 556, 557, 561, 1.0 mm.

type locality, the specific name a noun in apposition.

Description. Female. Carapace dark brown with white rim, clypeus orange. Sternum orange underlain by white pigment, darkest in center. Legs orange. Dorsum of abdomen white framed by black, sides with longitudinal white bands; venter black with some light pigment (Fig. 557). Carapace with one pair of dimples, shallow thoracic depression and wide rims. Abdomen with short anterior spines overhanging carapace and four pairs of large spines (Figs. 556, 557). Total length, 11.7 mm. Carapace, 4.1 mm long, 3.0 mm wide. First femur, 4.2 mm; patella and tibia, 4.5 mm; metatarsus, 2.6 mm; tarsus, 1.2 mm. Second patella and tibia, 4.0 mm; third, 2.6 mm. Fourth femur, 6.0 mm; patella and tibia, 5.0 mm; metatarsus, 3.3 mm; tarsus, 1.2 mm.

Male. Carapace dark brown, black on sides, shiny. Sternum brown. Legs shiny brown, first two femora darkest. Dorsum of abdomen brown, shiny; lighter brown anteriorly; lighter brown patch in waist region, and a lighter brown patch on each side posteriorly; venter dark; sclerotized areas brown. Carapace with shallow indistinct thoracic depression and one anterior pair of dimples. No coxal hook. Abdomen slightly constricted in middle, with a minute black nipple on each side anterior to constriction (Fig. 561). Total length, 6.0 mm. Carapace, 2.5 mm long, 1.4 mm wide. First femur, 1.8 mm; patella and tibia, 1.8 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm. Second patella and tibia, 1.5 mm; third, 1.0 mm. Fourth femur, 2.0 mm; patella and tibia, 1.7 mm; metatarsus, 1.1 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 9.7 to 13.3 mm.

Diagnosis. Micrathena balzapamba females differ from both *M. schreibersi* and *M. vigorsi* by the distinctive epigynum with its transverse ridge, the base of a torn-off scape (Figs. 558–560). A specimen received after completion of the illustrations had a small thin and soft scape. The paracymbium of the male palpus is flat, disk-shaped (Fig. 563), and the median apophysis has three spines (Fig. 562).

Distribution. Ecuador (Map 9).

Paratypes. ECUADOR: *Prov. Bolívar.* Balzapamba, 700 m, May 1938, ♀; 26 May 1938, ♀; 28 May 1938, ♂ (all W. Clarke-MacIntyre, AMNH); Naranjapata, 10 June 1958, ♀ (C. H. Dodson, CAS). *Los Ríos.* Playas de Montalvo, 20 April 1938, ♀ (W. Clarke-MacIntyre, AMNH); km 56 Quevedo to Santo Domingo, 28 Jan. 1973, ♀ (V. Brach, MCZ); Jauneche, 20 April 1984, ♀ (L. Avilés, MECN). *El Oro.* Palmales, ♀ (J. Sztolcman, PAN).

Micrathena schreibersi (Perty)
Plate 1; Figures 564–572; Map 9

Acrosoma schreibersi Perty, 1833: 194, pl. 38, fig. 9, ♀. Female from equatorial Brazil (ZSM), destroyed in the last war.

Acrosoma spinosum:—C. L. Koch, 1836: 56, pl. 210, ♀. Not *A. spinosa* (Linn.). Misidentification.

Plectana macracantha Walckenaer, 1841: 183. New name for *A. spinosum:*—C. L. Koch, thought misidentified.

?*Plectana duplicata* Walckenaer, 1841: 194. Female from Brazil. DOUBTFUL NEW SYNONYMY.

Plectana vespoides Walckener, 1841: 196. Specimen from Cayenne, French Guiana, lost. NEW SYNONYMY.

Acrosoma myrmeciaeformis Taczanowski, 1872: 280, pl. 6, fig. 30. Juvenile holotype from Cayenne, French Guiana (PAN), examined. NEW SYNONYMY.

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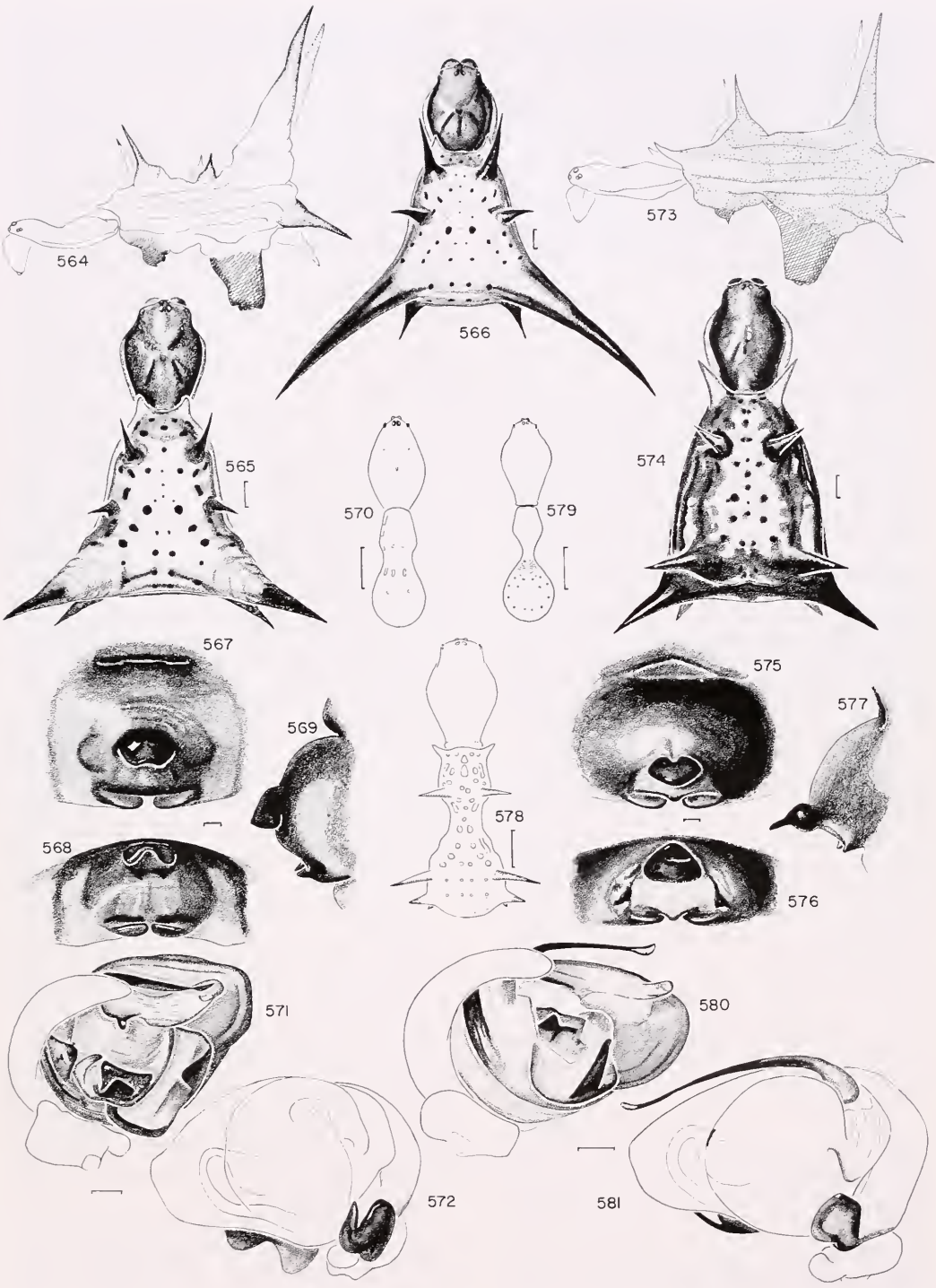
Figures 564–572. *Micrathena schreibersi* (Perty). 564–569. Female. 564. Lateral. 565, 566. Dorsal. 565. (Panama). 566. (Putumayo, Colombia). 567. Epigynum, ventral. 568. Epigynum, posterior. 569. Epigynum, lateral. 570–572. Male. 570. Dorsal. 571. Left palpus, mesal. 572. Palpus, lateral.

Figures 573–581. *Micrathena vigorsi* (Perty). 573–577. Female. 573. Lateral. 574. Dorsal. 575. Epigynum, ventral. 576. Epigynum, posterior. 577. Epigynum, lateral. 578. Juvenile. 579–581. Male. 579. Dorsal. 580. Palpus, mesal. 581. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 564–566, 570, 573, 574, 578, 579, 1.0 mm.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Acrosoma tenuis Taczanowski, 1873: 276, pl. 6, fig. 27. Juvenile female holotype and male paratype from Cayenne, French Guiana (PAN), examined. NEW SYNONYMY.

Acrosoma subtilis Taczanowski, 1873: 277, pl. 6, fig. 29. Juvenile syntypes from Saint Laurent de Maroni, French Guiana (PAN), examined. NEW SYNONYMY.

Micrathena schreibersi:—F. P.-Cambridge, 1904: 536, pl. 51, fig. 19, ♀. Reimoser, 1917: 137, pl. 9, fig. 27, ♀. Roewer, 1942: 963. Bonnet, 1957: 2877. Chickering, 1961: 452, figs. 157–168.

Ildibaha myrmeciaeformis:—Roewer, 1942: 953. Bonnet, 1957: 2296.

Micrathena subtilis:—Reimoser, 1917: 129. Roewer, 1942: 964. Bonnet, 1957: 2880.

Micrathena tenuis:—Reimoser, 1917: 136. Roewer, 1942: 965. Bonnet, 1957: 2880.

Micrathena coleophora Chamberlin and Ivie, 1936: 56, pl. 16, fig. 136, ♂. Male holotype from Barro Colorado Island, Panama (AMNH), examined. Synonymized by Chickering, 1961.

Micrathena lesserti Mello-Leitão, 1939: 70, figs. 48–50, ♀. Female holotype from Buenaventura, Colombia (NMB), examined. NEW SYNONYMY.

Synonymy. Walckenaer's *Plectana duplicata* and *P. vespoides* might both be this species. The first, a 15 mm-long female, has six posterior spines and two anterior, and a carapace with a yellow seam; *P. vespoides* is a male. The juvenile type of *Acrosoma myrmeciaeformis* is only 3.8 mm long, has ten spines and a constricted abdomen, as have juveniles of this species. *Acrosoma tenuis* is a juvenile female 5.4 mm long with spines and abdomen shaped like an adult and is accompanied by an adult male of this species. There are three juveniles of *Acrosoma subtilis*, 5.0 mm in total length with only eight spines, the anterolaterals small. They are probably this species. *Micrathena lesserti* is an adult female; *M. coleophora* is an adult male. Reimoser labeled some specimens of this species in collections as *M. spinosa*, a misidentification.

Description. Female from Panama. Carapace dark brown-black, rim white, clypeus orange. Sternum dark brown with orange edge, legs dark brown. Dorsum of abdomen white; orange to crimson at base of large spines. Black patches anteriorly and on sides; anterolateral spines white, others black; sides black with white longitudinal band; venter black with white marks around base of black spinneret cone (Figs. 565, 566). Carapace shiny and smooth, with an anterior pair of dimples and distinct pairs of grooves radiating from circular thoracic depression, rim distinct. Leg articles with tubercles. Abdomen with pair of small blunt spines overhanging carapace and four pairs of large spines (Figs. 564–566). Cone surrounding spinnerets longer than wide (Fig. 564). Total length, 11.5 mm. Carapace, 4.1 mm long, 3.4 mm wide. First femur, 5.3 mm; patella and tibia, 5.3 mm; metatarsus, 3.6 mm; tarsus, 1.3 mm. Second patella and tibia, 4.8 mm; third, 3.0 mm. Fourth femur, 6.5 mm; patella and tibia, 5.9 mm; metatarsus, 4.0 mm; tarsus, 1.2 mm.

Male from Panama. Carapace, sternum, legs, dorsum, venter and sides of abdomen orange; gray on venter anterior and posterior to spinnerets. Carapace shiny and smooth, with one pair of anterior dimples and a median thoracic mark; lacking rim. No coxal hook. First and second legs have some macrosetae. Abdomen with a constricted waist (Fig. 570). Total length, 4.7 mm. Carapace, 2.2 mm long, 1.4 mm wide. First femur, 1.6 mm; patella and tibia, 1.7 mm; metatarsus, 1.0 mm; tarsus, 0.6 mm. Second patella and tibia, 1.4 mm; third, 0.8 mm. Fourth femur, 1.4 mm; patella and tibia, 1.4 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 9.8 to 13.7 mm, males from 4.7 to 5.6 mm. The spines of some females from Colombia are much longer (Fig. 566) than those of Panamanian specimens. Some males have the carapace orange-rugose, others are much darker in color, almost black. Immatures have the third pair of spines minute or absent. Young males lack spines. An adult from Carillo, Costa Rica in the MCZ collection has the third pair of spines missing.

Note. Males and females are commonly collected together. Males and juveniles have the appearance of ants and may be mimics (Levi, in press). Chickering (1960)

first matched males with females, although he reported that Banks had already matched sexes but had not published on it.

Diagnosis. In females the area between the second and third pairs of spines is wider than long (Figs. 565, 566); in *M. vigorsi* longer than wide. The epigynum has a large median scale with the attached (anterior) end straight (Figs. 567–569); in *M. vigorsi* the attached end has a notch. The male's median apophysis lacks the prong present in *M. vigorsi* (Fig. 571).

Natural History. Micrathena schreibersi makes its web in forests and shady areas.

Distribution. Nicaragua to southeastern Brazil (Map 9).

Records. NICARAGUA: Musawas [Guabul], Waspuc River, Oct. 1955, ♂ (B. Malkin, AMNH). COSTA RICA: *Heredia Prov.* Puerto Viejo, La Selva (MCZ, ZMCR). *Limón.* Hamburg Farm, 2♀ (NMW); Siquirres (AMNH). *San José.* San José (MCZ); Carillo (MCZ). *Cartago.* Turrialba (MCZ, AMNH). PANAMA: *Bocas del Toro.* Río Changuinola, 16 km W of Almirante (AMNH). *Panamá.* Arraiján, (MCZ); Barro Colorado Isl., (MCZ); Pipeline Road (MCZ). Cerro Galero (MCZ). *Colón.* Pelucca, Boqueron Riv. (MCZ). LESSER ANTILLES: *Trinidad.* Mt. St. Benedict (CUC); Los Banguizales, Cedros (AMNH). VENEZUELA: *Est. Monagas.* Caripito (AMNH). *Miranda.* Pico Naiguatá (AMNH). *Bolivar.* Hato la Vergarena (AMNH). GUYANA: Kamakusa (AMNH); Kartabo (CUC). Sauri-wau Riv., Tacutu (AMNH). Upper Ireng Riv., Pakaraima Mts. (AMNH). Issororo (BMNH); Cannister Falls (BMNH); Yawakuri Riv., (BMNH). SURINAME: *Saramacca Prov.* Voltzberg-Raleighvallen Nature Reserve (MCZ); Paramaribo (MCZ). FRENCH GUIANA: Cayenne (PAN). COLOMBIA: *Dept. Meta.* Villavicencio (MCZ). *Cordoba.* Andagoga, Río Condato and Río San Juan (BMNH). *Antioquia.* Mutatá (MCZ). *Valle.* 20 km E of Buenaventura (MCZ). *Boyacá.* Río Suárez (AMNH). *Putumayo.* Pto. Asis (MCZ). ECUADOR: *Prov. Napo.* Pompeya Riv. (MCZ). Coca, Napo Riv. (MCZ); Limoncocha (MECN); Tarapuy (MECN). *Esmeralda.* Quininde (MECN). PERU: *Dept. Loreto.* Yurimaguas (AMNH); Iquitos (MCZ). *Ucayali.* La Frontera, Upper Utoquinia, 6♀ (AMNH); Ucayali Riv. (AMNH). *Huánaco.* Tingo María (EPC). *San Martín.* 20 km NE of Moyobamba (AMNH). BRAZIL: *Terr. Amapá.* Uaça (PAN); Rio Tracajatuba (IBSP); Santana, Rio Metapí (MEG); Serra do Navio (CAS); Vila Amazonias (MZSP). *Roraima.* Rio Branco (NMW); Mt. Roraima; Arabupus (AMNH). *Est. Pará.* Belém (MNHN, MCZ, IBSP, MEG, CAS); Canindé (AMNH); Rio Gurupi (MZSP); Tiriós, Paru (MZSP); Santarém (NMW). *Amazonas.* Manaus (MCZ, NRS, INPA); Rio Autaz, Capiranga (NRS); Lago Jacaré, Rio Solimões (MZSP). *Rondônia.* Pôrto Velho (AMNH). *Pernambuco.* Recife (MZSP); Mamanguape (MZSP); Tapera (IBSP). *Bahia.* Salvador (CAS, ZMK); Piraja (MCZ). *Minas Gerais.* Alto Rio Doce (MZSP). *Espírito Santo.* Rio São José (MZSP). *Santa Catarina.* Blumenau (NMW).

Micrathena vigorsi (Perty)
Figures 573–581; Map 9

Acrosoma vigorsii Perty, 1833: 194, pl. 38, fig. 8, ♀. Female from equatorial Brazil (ZSM), destroyed in last war. C. L. Koch, 1839: 123, fig. 520, ♀.

Acrosoma defensa Butler, 1873: 420. Female holotype in poor condition, formerly pinned, from Pará [Belém], Brazil (BMNH), examined. NEW SYNONYMY.

Ildibaha mutilloides Simon, 1895: 850, figs. 899, 900; 1896: 471. Male lectotype here designated and male and juvenile paralectotypes from Pebás [Dept. Loreto, Peru], Le Pará [Belém] and São Paulo de Olivença [Est. Amazon], Brazil (MNHN), examined. Roewer, 1942: 952. Bonnet, 1957: 2296. NEW SYNONYMY.

Micrathena vigorsi:—Petrunkevitch, 1910: 214, pl. 21, figs. 16–19, ♀. Reimoser, 1917: 132, pl. 8, fig. 24, ♀. Roewer, 1942: 966. Bonnet, 1957: 2881.

Micrathena defensa:—Reimoser, 1917: 133. Roewer, 1942: 956. Bonnet, 1957: 2865.

Synonymy. The specimen of *A. defensa* is an adult female. *Ildibaha mutilloides*

is a male with a constricted abdomen; its similarity to the male of *M. schreibersi* suggests that it is the male of *M. vigorsi*. Also, juveniles of *M. vigorsi* are known to have a constricted abdomen (Fig. 578).

Description. Female from Mato Grosso. Carapace brown-black with white rim. Sternum, legs brownish black. Dorsum of abdomen boldly marked black and white, first pair of spines white, others black; venter black. Carapace with a wide rim, three pairs of shallow dimples and a median thoracic mark. Legs corniculate. Abdomen with ten large spines, two pairs anterior, one posterodorsal, and two posterior (Figs. 573, 574). Total length, 14.5 mm. Carapace, 5.1 mm long, 4.0 mm wide. First femur, 6.5 mm; patella and tibia, 5.5 mm; metatarsus, 3.6 mm; tarsus, 1.4 mm. Second patella and tibia, 5.0 mm; third, 3.4 mm. Fourth femur, 7.2 mm; patella and tibia, 6.2 mm; metatarsus, 3.7 mm; tarsus, 1.4 mm.

Male lectotype of *I. mutilloides*. Carapace, sternum dark orange. Legs orange, the last femora darker. Abdomen with two white spots on anterior of dorsum. Carapace evenly domed, dull in appearance, no thoracic depression. First and second tibia and metatarsus with some macrosetae. Abdomen constricted in middle, lightly sclerotized on dorsum, sclerotized on venter in constricted area and in genital area (Fig. 579). No coxal hook. Total length, 4.8 mm. Carapace, 2.0 mm long, 1.2 mm wide. First femur, 1.4 mm; patella and tibia, 1.4 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.7 mm. Fourth femur, 1.4 mm; patella and tibia, 1.3 mm; metatarsus, 0.7 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 12.8 to 15.8 mm. The notch at the anterior of epigynum lobe is variable in size. An immature (? male) is illustrated by Figure 578.

Note. Males and females have not been collected together; their similarity to males and females of *M. schreibersi* suggests that they belong together (see above).

Diagnosis. Micrathena vigorsi differs from the similar *M. schreibersi* by having the distance between second and third pairs of spines greater than the width of the abdomen (Fig. 574), and by having the median lobe of the epigynum heart-shaped in ventral view, with an anterior notch (Figs. 575–577). Males differ by having a prong on the median apophysis (Fig. 580).

Distribution. Colombia to Brazil (Map 9).

Records. COLOMBIA: *Dept. Meta.* 20 km N of Río Muco, ♀ (W. Eberhard, MCZ). *Boyacá-Santander.* Río Suárez, 600–1,000 m, 11–12 Aug. 1946, 3♀ (AMNH). *Coquetá.* Río Orteguaza, Aug.–Sept. 1947, 2♀ (L. Richter, AMNH). ECUADOR: *Prov. Napo.* Coca and Napo Rivers, 24–30 April 1965, ♀ (L. Peña, MCZ); Limoncocha, 2 April 1983, ♀ (L. Avilés, MECN). PERU: *Dept. Loreto.* Iquitos, Feb.-May 1920, 8♀ (H. S. Parrish, MCZ); 1912, ♀ (AMNH). *Huánuco.* Cucharas, Feb.–Apr. 1954, 8♀, imm. (F. Woytkowski, EPC). *Lima.* Bosque Huacamayo, March 1969, ♀ (O. Meneses, IBSP). BRAZIL: *Est. Pará.* Belém, May 1927, 2♀ (Zerny, NMW). *Amazonas.* Rio Purus, Hyutanahã, 7 Feb. 1914, ♀ (A. Roman, NRS); 3–5 km E of Leticia [Colombia], 8 July 1977, ♀ (R. M. Shelley, MCZ); Tefé, Nov.–Dec. 1920, ♀ (H. S. Parrish, MCZ); Rio Uaupés, 2♀ (EPC). *Rondônia.* Abunã, March 1922, 3♀ (J. H. Williamson, MCZ), ♀ (J. W. Strohm, MCZ); Vila Murtinho, 5–7 April 1922, ♀, 28–30 March 1922, 2♀ (J. H. Williamson, MCZ). BOLIVIA: *Dept. Santa Cruz.* Buena Vista, Feb. 1951, 4♀ (Prosem, MULP).

The *militaris* Group

Females of the *militaris* group are characterized by having the abdomen squared or wider than long, with three to four pairs of spines, the third always largest (Figs. 598, 609, 621, 634); except in *M. swainsoni* (Fig. 639). The bulge of the epigynum has a pocket or groove on the posterior slope on each side of the tip (Figs. 584, 599, 622, 627, 635). These posterior

grooves are absent in *M. swainsoni* (Figs. 640, 641). The carapace is low, with a distinct thoracic depression but no dimples (Figs. 589, 620, 638). The book-lung covers lack a stridulating surface.

Males have the palpal tibia drawn out mesally into one or two fingers, as in the *spinosa* group (Figs. 595, 603, 614, 644). Unlike the *spinosa* group, the median apophysis forms two lobes (Figs. 587, 603) or spines (Figs. 595, 631); in *M. swainsoni* the median apophysis consists of three pieces (Fig. 644). Males lack the coxal hook and groove on the second femur.

The *spinosa* group may be a subgroup of the *militaris* group.

Species differ in the posterior view of the epigynum and in the form of spines and abdomen. Males differ in the length and curvature of the embolus, shape of the median apophysis and paracymbium.

KEY TO THE *MILITARIS* GROUP

Females

1. Third spine pair several times length of abdomen (Fig. 621); Amazon area, Map 10 ..... *cyanospina*
– Third spines as long or shorter than abdomen (Figs. 598, 634) 2
2(1) Abdomen rectangular, length more than twice width (Fig. 639); southeastern South America, Map 10 ..... *swainsoni*
– Abdomen subtriangular or wider than long (Figs. 609, 626) 3
3(2) Third pair of spines with tiny spine crowning a thicker portion (Figs. 633, 634); Amazon area, Map 10 ..... *hamifera*
– Third pair of spines without set off tip (Figs. 583, 609, 616) 4
4(3) Epigynum with a projecting posterior lobe, seen best in lateral view (Fig. 586); eastern North America to Panama, Map 10 ..... *sagittata*
– Epigynum otherwise (Figs. 591, 599); West Indies, South America 5
5(4) Abdomen with distinct fourth (or third) pair of spines behind the largest (Figs. 609, 616, 626); southeastern South America, Map 10 6
– Abdomen with at most a pair of denticles behind large spines (Fig. 589); West Indies, Map 10 8
6(5) Abdomen subtriangular, about as wide as long; last spine subequal to the one before (Fig. 626) ..... *furcata*
– Abdomen wider than long, with last spine distinctly smaller than penultimate (Figs. 609, 616) 7
7(6) Third pair of spines slender (Fig. 616); epigynum with tubercle on tip (Figs. 617–619) ..... *reimoseri*
– Third pair of spines thick (Fig. 609); epigynum without tubercle on tip (Figs. 610–612) ..... *lata*
8(5) Epigynum with a small light-colored transverse piece on tip (Fig. 599–601) ..... *militaris*
– Epigynum lacking transverse piece on tip (Figs. 591–593); Cuba, Map 10 ..... *banksi*

Males

Males of *M. cyanospina*, *M. hamifera*, *M. reimoseri* are unknown; male of *M. lata* of uncertain association.

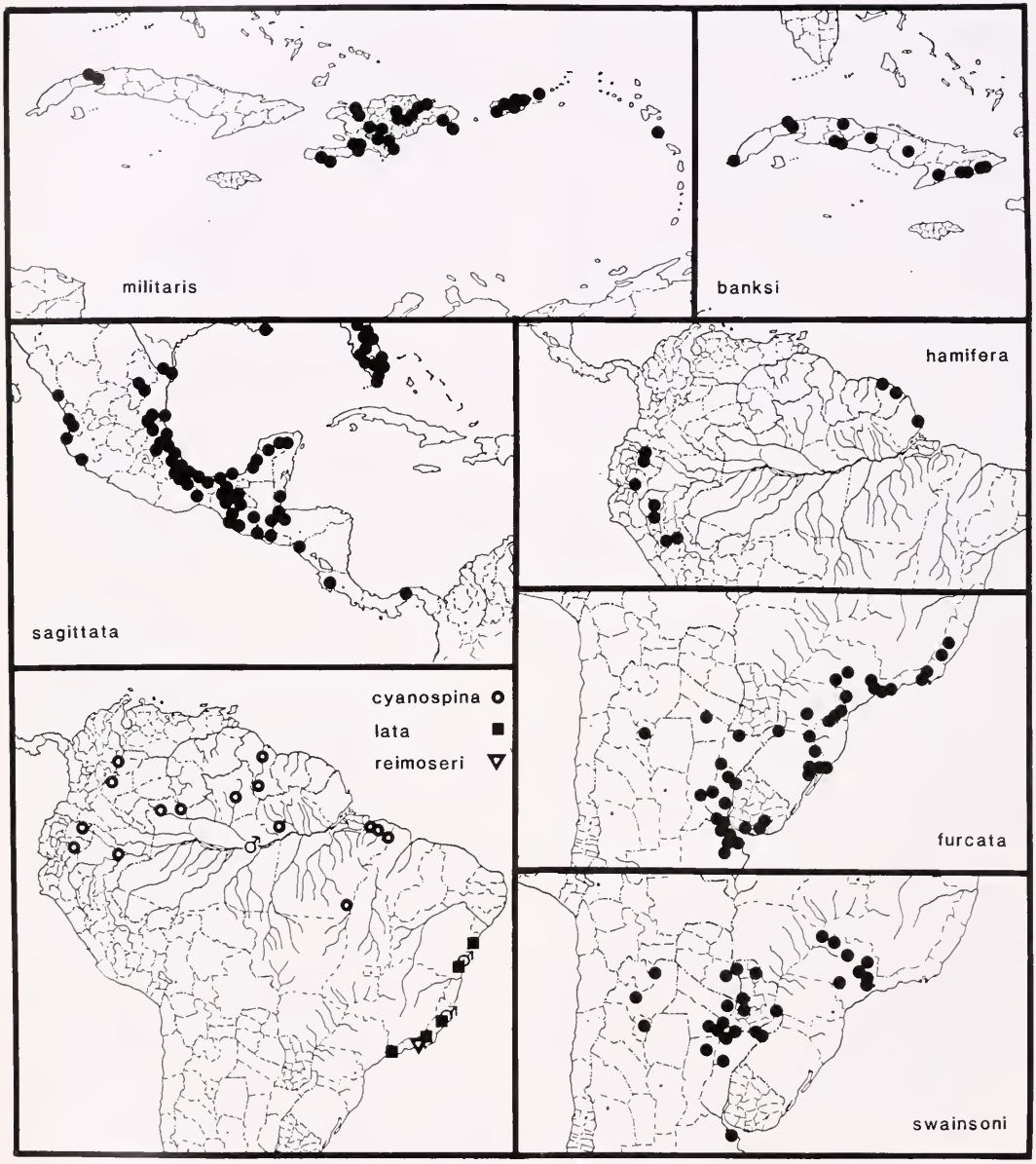
1. Abdomen with 8 sharp spines (Fig. 643); southeastern South America, Map 10 ..... *swainsoni*
– Abdomen with at most faint indications of spines (Figs. 602, 613) 2
2(1) Conductor a heavy curved hook (Fig. 614) ..... suspected male of *lata*
– Conductor otherwise 3
3(2) Embolus S-shaped, crossed by terminal apophysis (Fig. 631); southeastern South America, Map 10 ..... *furcata*
– Embolus straight, curved, or if S-shaped partly hidden by median apophysis (Figs. 587, 595, 603) 4
4(3) Embolus curved (Fig. 587); terminal apophysis small, not visible in lateral view (Fig. 588); eastern North America to Panama, Map 10 ..... *sagittata*
– Embolus only curved at proximal end (Figs. 595, 603); terminal apophysis visible in lateral view (Figs. 596, 604); West Indies, Map 10 5
5(4) Embolus slender and curved "above" cymbium (Figs. 595, 596); paracymbium large (Fig. 596); Cuba, Map 10 ..... *banksi*
– Embolus shorter, heavier, not curved above cymbium (Figs 603, 604); paracymbium small (Fig. 604); West Indies, Map 10 ..... *militaris*

Micrathena sagittata (Walckenaer) Figures 582–588; Map 10

Plectana sagittata Walckenaer, 1841: 174. The name was applied to an Abbot illustration of Georgia spiders.

Micrathena sagittata:—Levi, 1978: 430, figs. 41–54, map 2.

Note. My illustration of the male palpus (1978: fig. 5a) is quite inadequate. The median apophysis is bilobed. The S-shaped



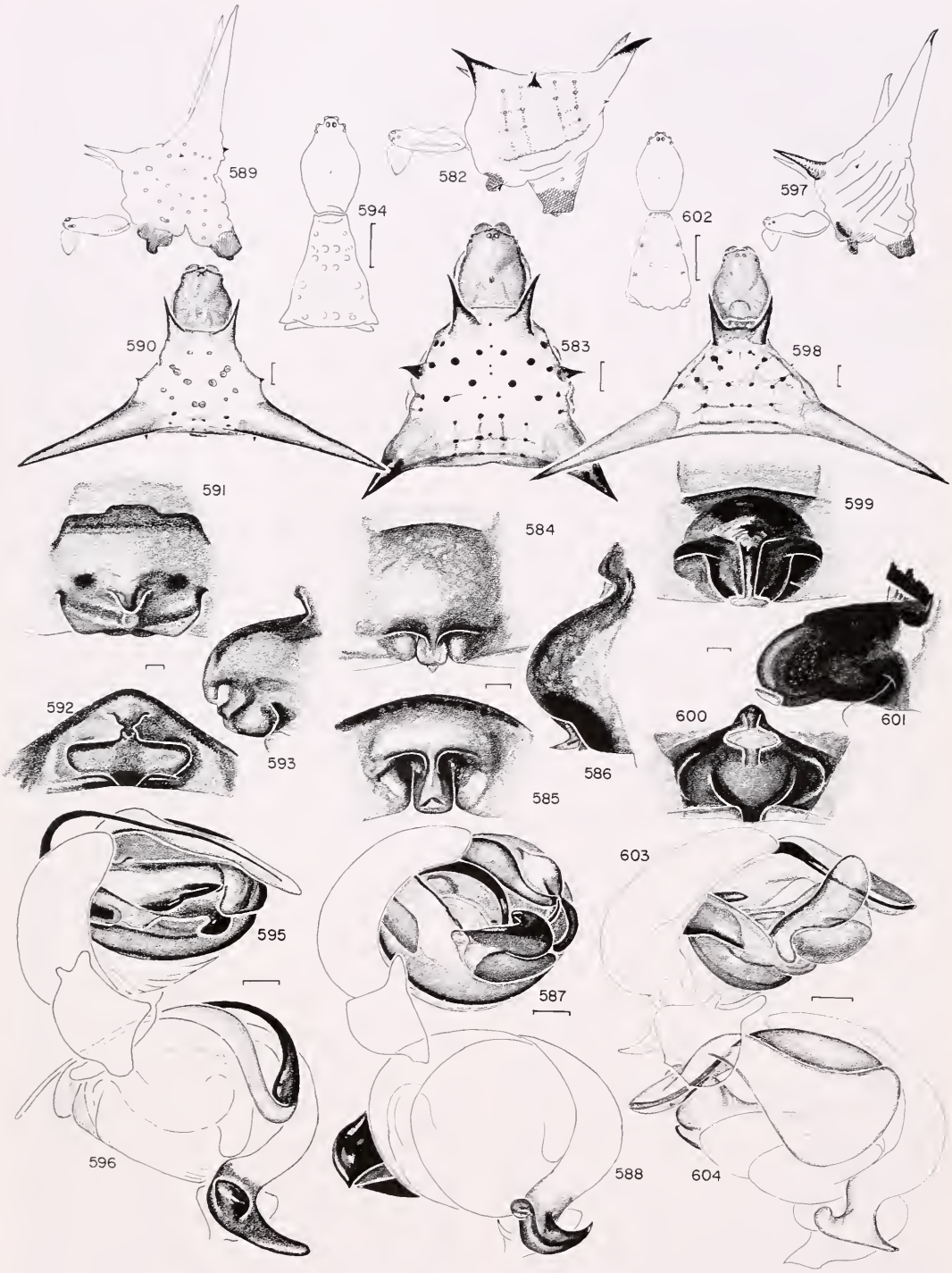
Map 10. Distribution of *Micrathena* species of the *militaris* group.

Figures 582–588. *Micrathena sagittata* (Walckenaer). 582–586. Female. 582. Lateral. 583. Dorsal. 584. Epigynum, ventral. 585. Epigynum, posterior. 586. Epigynum, lateral. 587–588. Male. 587. Left palpus, mesal. 588. Palpus, lateral.

Figures 589–596. *Micrathena banksi* n. sp. 589–593. Female. 589. Lateral. 590. Dorsal. 591. Epigynum, ventral. 592. Epigynum, posterior. 593. Epigynum, lateral. 594–596. Male. 594. Dorsal. 595. Palpus, mesal. 596. Palpus, lateral.

Figures 597–604. *Micrathena militaris* (Fabricius). 597–601. Female. 597. Lateral. 598. Dorsal. 599. Epigynum, ventral. 600. Epigynum, posterior. 601. Epigynum, lateral. 602–604. Male. 602. Dorsal. 603. Palpus, mesal. 604. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 582, 583, 589, 590, 594, 597, 598, 602, 1.0 mm.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black embolus is hidden in part by the upper lobe of the median apophysis, but its tip is visible touching the tip of the terminal apophysis. Both tips are supported by the conductor (Fig. 587). The palpal tibia is drawn out into one finger (Fig. 587) sometimes two (1978: fig. 53).

Variation. Females vary in total length from 7.5 mm to 9.4 mm, males from 4.3 to 5.5 mm. Females and juveniles from Central Mexico have a minute spine underneath the posterodorsal spine (Fig. 582). The thickness of spines varies.

Diagnosis. This is the only species of this group found in Mexico or Central America. Females differ from others of this group by having six dorsal spines (sometimes with a minute spine posteriorly; Figs. 582, 583), and by the shape of the epigynum: a pair of depressions behind eyebrowlike swellings, with a small projecting lobe on the septum (Figs. 584–586). The shorter, curved embolus, the single finger on the palpal tibia (Fig. 587), and the short, curved paracymbium (Fig. 588) separate males from those of *M. militaris* and *M. banksi.*

Distribution. Eastern North America to Panama, not in West Indies; West Indian references are all misidentifications (Map 10).

Records. MEXICO: *Est. Tamaulipas.* Antigue Morelos. *Nuevo León.* Montemorelos. *San Luis Potosí.* Valles; San Joaquín; Tamazunchale; near Xilitla; 5 km W El Naranjo. *Sinaloa.* San Ignacio. *Nayarit.* Tepic. *Jalisco.* Puerto Vallarta; San Blas. *Colima.* Armeria. *Veracruz.* Tres Valles; Veracruz; Córdoba; Martínez de la Torre; Papantla; Lago Catemaco; Fortín; La Buena Ventura; Tlacojalpan; Tuxtilla; Tuxpan; Istmo de Tehuantepec; Tlapacoyan; Tecolutla; Potrero; Jalapa; Coscomatepec; N of Catemaco. *Puebla.* Huauchinango; Villa Juárez. *Oaxaca.* Palomares; Papaoapan; Paso Real, Río Tonto. *Tabasco.* Cárdenas; 2.4 km of Teapa; Frontera; Teapa; Comalcalco. *Campeche.* Campeche; San José. *Yucatan.* Valladolid; Chichen Itza; 3 km E Chichen Itza; Uxmal. *Chiapas.* Iztacomitán; Chiapa; Huehuetán; Huixtla; La Zacualpa; Palenque ruins; El Vergel; Simojove. GUATEMALA: *Dept. Izabal.* Quirigua; Bananera; Livingston. *Alta Verapaz.* Tucuru. *Suchitepéquez.* Chicacao, El Naranjo; Moca; Variedades. *Chimatenango.* Yepocapa. *San Marcos.* Ayutla. BELIZE: *Cayo Distr.* Mt. Pine Ridge. HONDURAS: *Dept. Copán.* Copán. EL SALVADOR: Laguna Apastepeque; Quezaltepeque. NICARAGUA: Consiquina slope. COSTA RICA: *Prov. Guanacaste.* Bebedero, 20 June 1930, ♂ (E. Reimoser, NMW). PANAMA: *Prov. Panamá.* Barro Colorado Island, Gatún Lake, 4 Aug. 1935 (J. D. Hood, AMNH), 10 Feb 1936 (W. J. Gertsch, AMNH).

Micrathena banksi new species
Figures 589–596; Map 10

Micrathena militaris:—Bryant, 1940: 376, fig. 154, ♀ (not figs. 140, 145). Chickering, 1964: 269, figs. 45–47, ♀ (not figs. 41–44). Misidentification, not *militaris* Fabricius.

Micrathena cubana:—Bryant, 1940: 374, fig. 144, ♂. Chickering, 1964: 256, figs. 8–10, ♂. Misidentification, not male of *cubana* Banks.

Holotype. Female with one female paratype from Loma del Gato, 800 to 1,000 m, Sierra de Cobre, Santiago Province, Cuba (S. C. Bruner, MCZ). The species is named after Nathan Banks.

Description. Female. Carapace, sternum orange-brown. Legs orange. Dorsum of abdomen white with large spines orange; venter and sides black with large white spots. Carapace smooth, with a distinct light rim and a quite shallow thoracic depression (Figs. 589, 590). Sternum sculptured, with three pairs of lateral tubercles and a posterior median tubercle. Abdomen with two pairs large spines, posterior one larger, and two pairs minute denticles, one on side between large spines and one on posterior face of the abdomen (Figs. 589, 590). Total length, 8.0 mm. Carapace, 3.6 mm long, 3.0 mm wide. First femur, 4.3 mm; patella and tibia, 3.6 mm; metatarsus, 2.4 mm; tarsus, 1.2 mm. Second patella and tibia, 3.3 mm; third, 1.9 mm. Fourth femur, 4.5 mm; patella

and tibia, 3.8 mm; metatarsus, 2.5 mm; tarsus, 0.9 mm.

Male. Carapace dark brown, lighter in midline. Sternum black with white pigment all around. Coxae and femora blackish brown, distal article of legs lighter. Dorsum of abdomen blackish with pair of white spots; venter black; posterior face of abdomen white. Carapace corniculate, with a shallow median thoracic depression. Femora corniculate. Abdomen triangular, sides undulating (Fig. 594). Total length, 5.0 mm. Carapace, 2.2 mm long, 1.4 mm wide. First femur, 1.3 mm; patella and tibia, 1.2 mm; metatarsus, 0.8 mm; tarsus, 0.5 mm. Second patella and tibia, 1.1 mm; third, 0.7 mm. Fourth femur, 1.4 mm; patella and tibia, 1.2 mm; metatarsus, 0.5 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 6.5 to 7.7 mm. The small denticles on the abdomen are sometimes missing.

Diagnosis. The female differs from *M. militaris* by having eight spines: four large ones and four denticles which are sometimes absent (Figs. 589, 590). The epigynum differs by lacking a transverse, light colored, posterior bar at its tip; unlike *M. militaris* and *M. sagittata* it has a posterior transverse sclerite (Figs. 591–593). The male differs from *militaris* by the longer, curved embolus (Figs. 595, 596) and by the recurved hook-shaped median apophysis (Fig. 596).

Natural History. Only one specimen comes with habitat notes: forest.

Distribution. Cuba (Map 10).

Paratypes. CUBA: *Prov. La Havana.* Havana, 1915, ♀ (T. Barbour and Brooks, MCZ); Santiago de las Vegas, 20 March 1944 (L. Gonzalez, AMNH). *Villa Clara.* Vega Alta, ♀ (P. Bermudez, CUC). *Cienfuegos.* Soledad, Cienfuegos, 1927, ♀, ♂ (several records); Sierra Trinidad, Buenos Aires, July, 2 imm. (Parsons, MCZ). *Camagüey.* San Blas, 13 Aug. 1932, ♀ (B. B. Leavitt, MCZ). *Sancti Spiritus.* Jobosi. *Santiago de Cuba.* Puerto Boniato, 7 April 1946, ♀ (P. Alayon, AMNH); Loma del Gato, Sierra del Cobre, 800–1,000 m, ♂ (S. C. Bruner, MCZ). *Guantánamo.* Pan de Palenque, 1 Aug. 1955, imm. (A. F. Archer, AMNH); Monte Verde, Guantánamo, 30 Nov. 1971, ♀ (O. Garrido, J. de la Cruz, CASH); Guantánamo, 1913, ♀ (T. Barbour, MCZ). *Granma.* Sierra Maestra, 15–20 May 1948, ♀ (J. Acuña, MCZ). *Pinar del Río.* Guanahacabibes, ♀ (MCZ).

Micrathena militaris (Fabricius)
Figures 597–607; Map 10

Aranea militaris Fabricius, 1775: 416. Specimen from America, lost (Zimsen, 1964). The type locality is here restricted to Hispaniola.

Aranea armata Olivier, 1789: 205. Specimen from unknown locality, lost.

Aranea taurus Fabricius, 1793: 424. Specimen from Insula St. Domingo.

Plectana furcata Walckenaer, 1841: 176. New name for *Araneus armata* and *A. taurus* from Santo Domingo [not *Micrathena furcata* (Hahn) 1833].

Acrosoma armata:—C. L. Koch, 1845: 65, fig. 885, ♀.

Micrathena armata:—Reimoser, 1917: 152. Franganillo, 1936: 98, fig. 51, ♀.

Micrathena militaris:—Petrunkevitch, 1926: 53, figs. 12–15, ♀; 1930: 257. Bryant, 1940: 376, figs. 143, 145, ♂ (not fig. 154, ♀). Chickering, 1964: 269, figs. 41–44, 49–50, ♀, ♂ (not figs. 45–47).

Micrathena sagittata:—Petrunkevitch, 1930: 259, records only; misidentification, not *M. sagittata* (Walckenaer).

Synonymy. Fabricius described *M. militaris* as having four dorsal spines, the posterior long and open (patentibus). I am here following American authors (Petrunkevitch, Bryant and Chickering), but restrict the type locality of *M. militaris* to Hispaniola.

In the Simon collections in Paris are 11 specimens from Santo Domingo marked *M. armata* which are this species. The Berlin Museum also has old specimens of this species from Puerto Rico and Port au Prince, Haiti marked *M. armata.* Reimoser (1917) considered this species to be *M. armata,* and *M. militaris* to be a four-spined species close to *M. sexspinosa* from South America. But the *M. sexspinosa* group of species have four to six spines in addition to a forked abdomen.

Walckenaer considered *A. armata* and *A. taurus* to be the same, and synony-

mized the names by giving them a new name: *P. furcata.*

Description. Female from Dominican Republic. Carapace orange. Sternum orange with some black maculations. Legs blackish. Dorsum of abdomen white to yellow, anterior spines orange to black, posterior spines orange; venter with yellow-white patches and black. Carapace with a fine rim and a median thoracic depression. Lateral eyes more than their diameter apart. Abdomen with two pairs of large spines and usually a tiny tooth on each side (Figs. 597, 598). Total length, 7.5 mm. Carapace, 3.0 mm long, 2.3 mm wide. First femur, 3.3 mm; patella and tibia, 3.0 mm; metatarsus, 2.0 mm; tarsus, 1.1 mm. Second patella and tibia, 2.6 mm; third, 1.7 mm. Fourth femur, 3.5 mm; patella and tibia, 2.9 mm; metatarsus, 1.9 mm; tarsus, 0.9 mm.

Male. Carapace orange-brown. Sternum orange with dark mark in center. Legs orange. Dorsum of abdomen whitish with some paired black patches; venter white and black. Carapace shiny with thoracic depression. Abdomen subtriangular with lobes on posterior margin (Fig. 602). Total length, 4.0 mm. Carapace, 1.8 mm long, 1.0 mm wide. First femur, 1.2 mm; patella and tibia, 1.2 mm; metatarsus, 0.7 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.6 mm. Fourth femur, 1.6 mm; patella and tibia, 0.9 mm; metatarsus, 0.5 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 6.0 to 8.1 mm, males from 3.4 to 5.4 mm. The smallest specimens came from Cuba. The tiny teeth on the sides of the abdomen may be missing. The posterolateral spines vary widely in shape: often long and slender (Fig. 598) sometimes much shorter and thicker, giving the abdomen a different profile. The proportions of the abdomen of males are also quite variable.

Note. Several males have been collected at collecting sites of females. It is the only species of the *militaris* group in most of the area. The male embolus and terminal apophysis remain in the epigynum after mating (Figs. 605–607).

Diagnosis. Females are separated from *Micrathena banksi* and *M. sagittata* by the lightly sclerotized small transverse bar making up the tip of the epigynum (Figs. 599–601). The male has an unusual cylindrical tooth above the radix (Fig. 603); the length of the embolus, intermediate between that of *M. banksi* and *M. sagittata*, distinguishes the species. The lobed median apophysis distinguishes this species from *M. banksi* (Fig. 603).

Distribution. Cuba, Hispaniola (common), Puerto Rico to Dominica (Map 10).

Records. CUBA: *Prov. La Havana.* Havana, ♀ (AMNH). Santiago del Vegas, 2♂ (MCZ). HAITI: Cap Haïtien, ♀, ♂ (MCZ, CUC); Grand Rivière, ♀ (MCZ); Pétionville, ♀ (MCZ); NE of La Hatte, ♀ (MCZ); Port-au-Prince, ♀, ♂ (MCZ); Furcy, ♀ (MCZ); Diquini, ♀, ♂ (MCZ); Ennery, ♀ (MCZ); 32 km NW of Les Cayes, ♀ (MCZ); Les Cayes, Les Platons, ♀ (MCZ); Kenscoff, 3♀ (AMNH). DOMINICAN REPUBLIC: *Prov. La Vega.* Montanas Cibao, Cordillera Central, ♀, ♂ (AMNH); Loma Cibao, Cord. Central, ♀, ♂ (MCZ); Constanza, Cord. Central, ♂ (MCZ); Jarabacoa, ♀, ♂ (AMNH); Bonao, ♀ (MNSD). *Samana.* Sanchez, ♀, ♂ (MCZ, AMNH). *La Romana.* La Romana, ♀ (AMNH); Isla Saona, Catuano, 3♀ (MNSD). *Duarte.* Villa Riva, ♀ (AMNH); Loma Quita Espuela, 830 m, San Francisco de Macaris, ♀ (MNSD). *Santiago.* S of Santiago, ♀ (MCZ). *Barahona.* Colonia Ranfis, Loma los Pinos, Trujilo Valdez, ♀, ♂ (AMNH); San Lorenzo, ♀ (AMNH); Mt. Busú, Sierra Martín Guarcía, 1,200–1,300 m, ♀ (MCZ); peak of Monte Busú, 1,200–1,300 m, ♀ (MCZ); Polo, ♀ (MNSD). *San Juan.* El Cercado, 3♀ (MNSD); La Hermita, 3♀ (MNSD). *Independencia.* Entre Negba, ♀ (MNSD); Duvergé, ♀ (MNSD). *Estrelleta.* Elias Piña, Río Artibonito, 3♀ (MNSD). *Sánchez Ramírez.* Mina Puebla Viejo, Hatillo, 8♀ (MCZ). PUERTO RICO: Monte El Estado, Maricao, ♂ (MCZ); San Sebastian, ♀ (MCZ); Bosque Estatal de Maricao, ♀

(MCZ); San Juan, ♀ (CUC); Arecibo, Reserva Forestal Cambalache, ♀ (MCZ); Aibonito, ♀, 2♂ (AMNH). La Gloria, Luquillo Range, ♀ (PMYU). VIRGIN ISLANDS: St. Thomas, ♀ (PMYU). DOMINICA: pass on Grand Bay Road, 23 June 1937, 2 juv., ♂ (Roys, MCZ).

Micrathena lata Chickering
Figures 608–615; Map 10

Micrathena lata Chickering, 1960a: 6, figs. 8–12, ♀. Female from Teresópolis, Est. Rio de Janeiro, Brazil (MCZ), examined.

Description. Female. Carapace orange with head lightest except in midline. Sternum, legs orange. Dorsum of abdomen orange-yellow; black spot on anterior of each posterolateral spine; venter orange. Carapace with median thoracic mark, lacking rim in dorsal view, thorax fairly high (Fig. 608). Abdomen quite high (Fig. 608), wider than long (Fig. 609), with a large posterodorsal spine on each side, a pair of anterior spines overhanging the carapace, a small spine in between on lateral margin, and one below each long posterodorsal spine (Fig. 609). Abdomen with waxy texture. Total length, 7.0 mm. Carapace, 3.0 mm long, 2.4 mm wide. First femur, 3.1 mm; patella and tibia, 2.7 mm; metatarsus, 1.7 mm; tarsus, 0.9 mm. Second patella and tibia, 2.7 mm; third, 1.7 mm. Fourth femur, 3.4 mm; patella and tibia, 2.7 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm.

Male. Carapace, legs brown. Sternum darker brown than coxae. Dorsum of abdomen white with black markings. Venter black around spinnerets, gray on sides with two white spots on posterolateral corner of each side. Carapace with quite indistinct thoracic depression (Fig. 613). No coxal hook. Abdomen trapezoidal, widest posteriorly. Total length, 4.2 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 1.2 mm; patella and tibia, 1.3 mm; metatarsus, 0.7 mm; tarsus, 0.4 mm. Second patella and tibia, 1.2 mm; third, 0.9 mm. Fourth femur, 1.6 mm; patella and tibia, 1.4 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 7.0 to 8.2 mm, males from 3.9 to 4.2 mm.

Note. Males have not been collected with females. The male belongs to the same species group but might be *M. reimoseri.*

Diagnosis. Micrathena lata differs from *M. reimoseri* by having longer fourth pair of spines (Fig. 609) and in details of the epigynum (Figs. 610–612). The male suspected to be this species can be separated from others of this species group by the elaborately shaped and lobed palpal tibia, by the large hook of the conductor, and by the fine spine facing the embolus at the base of the median apophysis (Figs. 614, 615).

Records. BRAZIL: *Est. Amazonas.* Manaus, 1 Oct. 1962, ♂ (K. Lenko, MZSP). *Bahia.* Itamarahú, 7 Dec. 1978, 2♀ (J. Santos, FZRS); Camacari, 3 Dec. 1977, ♀ (J. Santos, FZRS), 2 Dec. 1977, ♀ (F. Santos, FZRS); Urucuca, ♂ (F. Santos, FZRS). *Espírito Santo.* Santa Teresa, 29 Sept. 1942, ♂ (B. A. Soares, MZSP). *São Paulo.* Salesópolis, 28 Feb. 1967, ♀ (D. Biasi, MZSP).

Micrathena reimoseri Mello-Leitão
Figures 616–619; Map 10

Micrathena reimoseri Mello-Leitão, 1935: 97, fig. 14, ♀. Female lectotype here designated and one paralectotype from Petrópolis, Est. Rio de Janeiro, Brazil (MNRJ), examined. Roewer, 1942: 962. Bonnet, 1957: 2875.

Description. Female lectotype. Carapace orange with median dark gray line. Sternum orange. Legs orange; distal articles much darker. Dorsum of abdomen orange with a black spot on each lateral spine and tiny white dots; venter orange with tiny white spots. Carapace with distinct thoracic depression and a shallow dent anterior to thoracic depression. Abdomen much wider than long (Fig. 616). Total length, 7.5 mm. Carapace, 3.1 mm long, 2.7 mm wide. First femur, 3.6 mm; patella and tibia, 3.4 mm; metatarsus, 2.0

mm; tarsus, 0.9 mm. Second patella and tibia, 3.1 mm; third, 2.2 mm. Fourth femur, 3.8 mm; patella and tibia, 3.3 mm; metatarsus, 2.2 mm; tarsus, 0.9 mm.

Note. Paralectotype has a wider abdomen and a more anterior projecting bulge on the epigynum, quite distinct from the lectotype. I assume that this is a variable species, and that *Micrathena lata* Chickering might prove to be a synonym.

Diagnosis. This species differs from *M. lata* by having the fourth pair of spines minute (Fig. 616, in *M. lata* they are half the length of the third spine) and in having a small knob on the tip on the epigynum (Figs. 617–619). They differ from others of the species group by the wide abdomen (Fig. 616).

Micrathena cyanospina (Lucas)
Figures 620–624; Map 10

Epeira cyanospina Lucas, 1835: 70, pl. 149, fig. 3, ♀. Female specimens from Java (an error), lost.
Micrathena cyanospina:—Reimoser, 1917: 139. Roewer, 1942: 956. Bonnet, 1957: 2865.

Description. Female from Rio Branco, Brazil. Carapace dark orange; eye region orange without black pigment. Sternum, legs orange. Dorsum of abdomen black with transverse orange-white pigment patches (Fig. 621); long spines iridescent bluish; sides orange-white; venter with white patch behind epigynum, a black ring around the spinnerets and a white ring more distally around cone of spinnerets. Carapace with thoracic depression, low thorax, no dimples or rim (Figs. 620, 621). Total length, 10.0 mm. Carapace, 4.3 mm long, 3.8 mm wide. First femur, 5.8 mm; patella and tibia, 5.4 mm; metatarsus, 3.5 mm; tarsus, 1.3 mm. Second patella and tibia, 4.9 mm; third, 3.1 mm. Fourth femur, 6.9 mm; patella and tibia, 5.8 mm; metatarsus, 3.6 mm; tarsus, 1.4 mm. Spines about 32 mm long.

Variation. Females vary in total length from 10.0 to 11.7 mm; length of third spine varies from 25 to 32 mm. Smaller sized individuals have relatively shorter spines than do larger ones. The epigynum in posterior view has the transverse swellings variable in size. One specimen had the light patches of the dorsum of the abdomen sclerotized.

Note. The male is unknown.

Diagnosis. The long third spine, twice to three times body length (Fig. 621), separates this species from others of the group.

Distribution. Amazon region (Map 10).

Records. GUYANA: *Berbice Co.* Canje River, ♀ (G. Bentley, AMNH). *Essequibo.* ultimate source of Rewa [Illiwa Riv.], Oct. 1911, ♀ (J. O. Ogilvie, MCZ). COLOMBIA: *Dept. Meta.* Monte Redonado, 45 km W of Villavicencio, June 1947, imm. (L. Richter, AMNH); Villavicencio, July 1938, imm. (H. Dybas, AMNH), May 1945, ♀ (AMNH). *Boyacá.* Río Dpan, 850–950 m, imm. (AMNH). ECUADOR: *Prov. Napo.* Río Tarapuy at Aguas Negras, Nov. 1982, ♀ (L. Avilés, MCZ). *Pastaza.* Río Pastaza, ♀ (Olalla, AMNH). PERU: *Dept. Loreto.* Mishana, 2 Nov. 1974, ♀ (P. A. Holzbauer, MPM). BRAZIL: *Terr. Roraima.* Rio Branco, ♀ (NMW). *Est. Pará.* Belém, ♀ (H. H. Smith, MCZ); 45 km E of Canindé, ♀ (B. Malkin, AMNH); Canindé (several collections, AMNH); Rio Guamá, Aug. 1952, ♀ (IBSP); Conceigão do Araguaia, Jan. 1983, ♀ (A. Harada, CNDC); Rio Gurupi, May 1963, ♀ (B. Malkin, MZSP);

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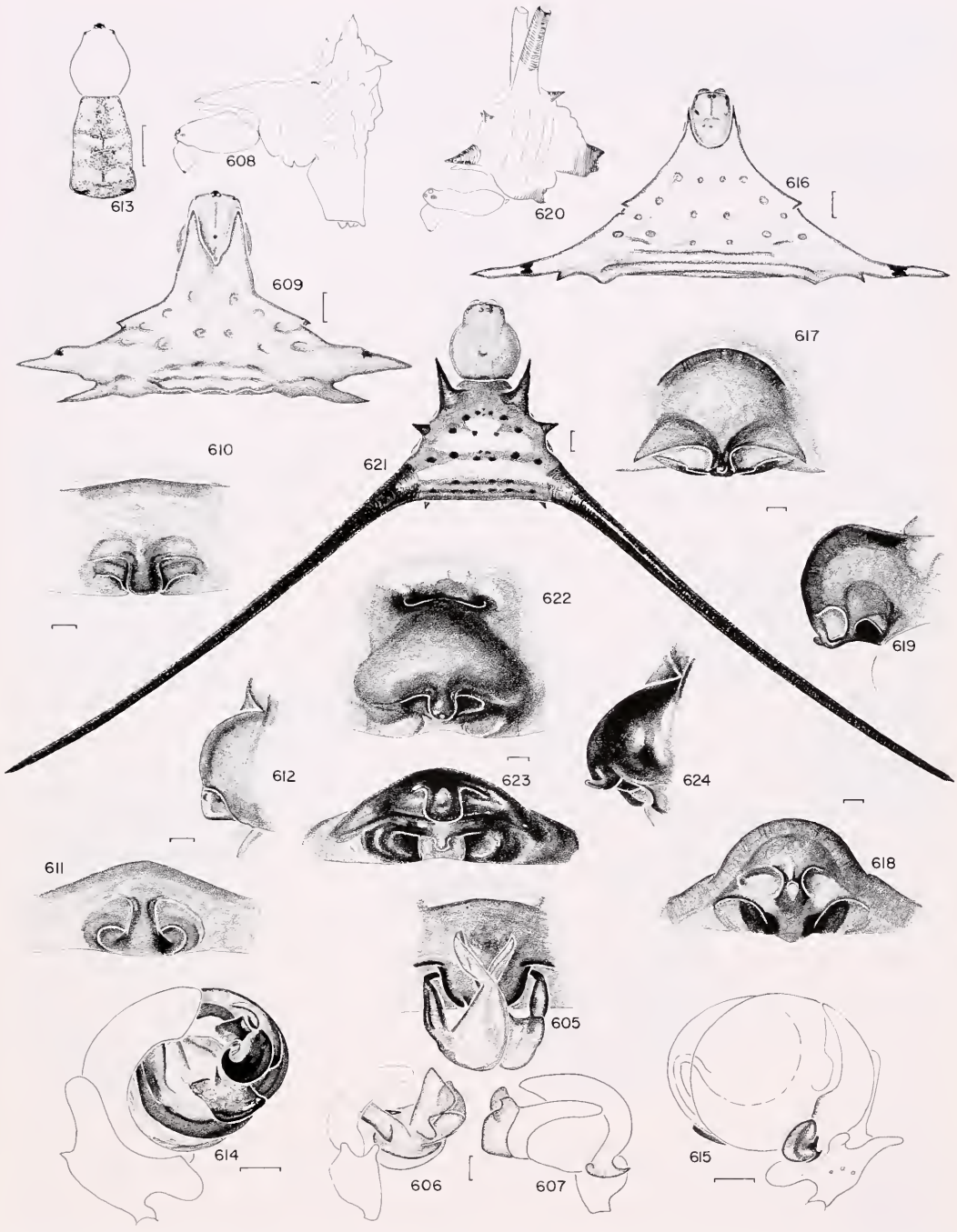
Figures 605–607. *Micrathena militaris* (Fabricius). 605. Epigynum with male emboli and terminal apophyses. 606, 607. Mated male left palpus, embolus and terminal apophysis torn off. 606. Palpus, mesal. 607. Palpus, lateral.

Figures 608–615. *Micrathena lata* Chickering. 608–612. Female. 608. Lateral. 609. Dorsal. 610. Epigynum, ventral. 611. Epigynum, posterior. 612. Epigynum, lateral. 613–615. Male. 613. Dorsal. 614. Palpus, mesal. 615. Palpus, lateral.

Figures 616–619. *Micrathena reimoseri* Mello-Leitão, female. 616. Dorsal. 617. Epigynum, ventral. 618. Epigynum, posterior. 619. Epigynum, lateral.



Figures 620–624. *Micrathena cyanospina* (Lucas), female. 620. Lateral. 621. Dorsal. 622. Epigynum, ventral. 623. Epigynum, posterior. 624. Epigynum, lateral.

Scale lines. 0.1 mm, except Figures 608, 609, 613, 616, 620, 621, 1.0 mm.

Cachimbo, Nov. 1955, June 1965, 5♀, imm. (MZSP). *Amazonas.* Uaupés, March 1952, ♀ (J. Falco, IBSP); Rio Negro, Umarituba, 19 April 1924, ♀ (A. Roman, NRS).

Micrathena furcata (Hahn)
Figures 625–632; Map 10

Epeira furcata Hahn, 1822, pl. 4, fig. B, ♀. Specimen from Cayenne (locality probably an error).

Acrosoma bifurcata Hahn, 1834: 65, fig. 158, ♀. Female from Brazil, lost. C. L. Koch, 1839: 124, fig. 521, ♀.

Plectana difissa Walckenaer, 1841: 181. New name for *Acrosoma bifurcatum*—C. L. Koch, thought misidentified. NEW SYNONYMY.

?*Plectana flabellata* Walckenaer, 1841: 192. Female from South America. DOUBTFUL NEW SYNONYMY.

Acrosoma gilvulum C. L. Koch, 1845: 67, fig. 886, ♀. Female from Brazil in the collection of Prof. Reich, Berlin, lost. First synonymized with *difissa* by Reimoser, 1917.

Micrathena difissa:—Reimoser, 1917: 113, pl. 6, fig. 15, ♀. Roewer, 1942: 957. Bonnet, 1957: 2866.

Micrathena bifurcata:—Roewer, 1942: 954. Bonnet, 1957: 2862.

Micrathena amplexa Mello-Leitão, 1944a: 3: 332, figs. 17, 18, ♂. Male holotype with left palpus missing, right expanded, from Tigre, Buenos Aires Prov., Argentina (MULP), examined. NEW SYNONYMY.

Synonymy. In 1822 Hahn illustrated this species, which he called *Epeira furcata.* It appeared on the same plate as another species, *E. sexspinosa*; unfortunately, the figure legends were reversed, and the illustration of *furcata* labeled "*Epeira sexspinosa.*" In 1834 Hahn used the same illustration for *A. bifurcata*, referring in the text to the mislabeled figure 158 ("A. 6-spinosa in Tabula"). Thus, while the initial reversal remains uncorrected, the reader is made aware of it in the 1834 publication. C. L. Koch in 1835 published a better illustration and description because of the poor condition of Hahn's specimen (C. L. Koch, 1839). Walckenaer considered Koch's illustration a different species and gave it the name *difissa.* Hahn's specimen of *Epeira furcata*, although pinned and shrivelled, was undoubtedly this species, as is C. L. Koch's figure 521. The spines and the black bands on the carapace that were illustrated are diagnostic. Both Roewer and Bonnet list the name *M. bifurcata* (Hahn) and the name *furcata* as a synonym of *armata.* Mello-Leitão described the male as *M. amplexa.*

Walckenaer's *M. flabellata* was 7.8 mm long, the abdomen elongate triangular, divided into two lobes posteriorly, each lobe with two spines; another pair of spines hangs over the carapace. It might be this species.

Description. Female. Carapace yellow with a median and two paraxial black lines. Sternum yellow. Legs yellow with a black line on the first, second and third femur ventrally. Dorsum of abdomen white with a posterolateral spine having a black patch on anterior face, white on posterior; venter black around spinnerets and with paired white patches. Carapace relatively low in thorax, with a thoracic depression; no rim or dimples. Abdomen triangular, width and length equal, with four pairs of spines: anterior pair overhanging carapace, a small tooth on each side, and two posterolaterally of almost equal length (Figs. 625, 626). Total length, 7.3 mm. Carapace, 3.0 mm long, 2.5 mm wide. First femur, 2.7 mm; patella and

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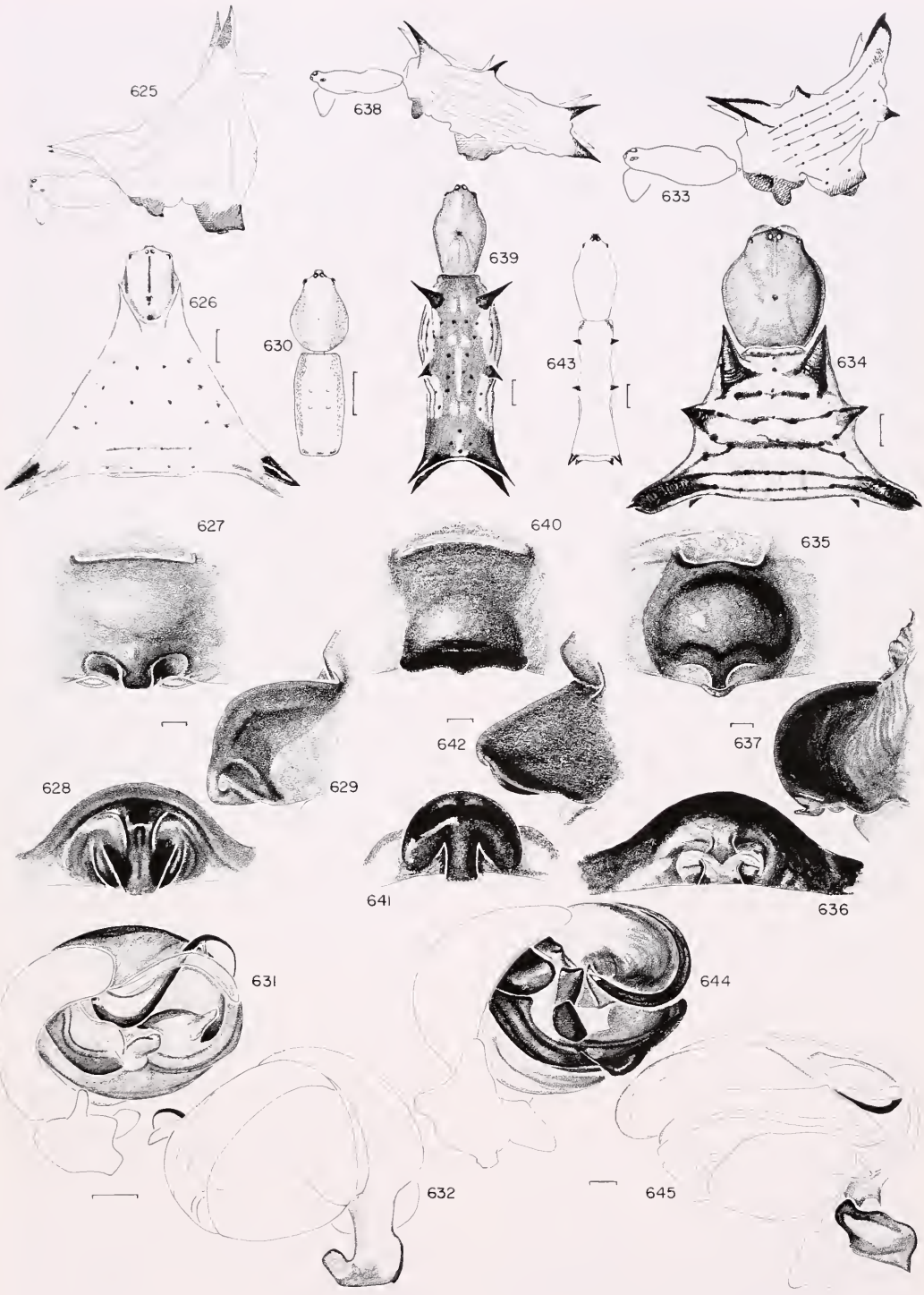
Figures 625–632. *Micrathena furcata* (Hahn). 625–629. Female. 625. Lateral. 626. Dorsal. 627. Epigynum, ventral. 628. Epigynum, posterior. 629. Epigynum, lateral. 630–632. Male. 630. Dorsal. 631. Left palpus, mesal. 632. Palpus, lateral.

Figures 633–637. *Micrathena hamifera* Simon, female. 633. Lateral. 634. Dorsal. 635. Epigynum, ventral. 636. Epigynum, posterior. 637. Epigynum, lateral.

Figures 638–645. *Micrathena swainsoni* (Perty). 638–642. Female. 638. Lateral. 639. Dorsal. 640. Epigynum, ventral. 641. Epigynum, posterior. 642. Epigynum, lateral. 643–645. Male. 643. Dorsal. 644. Palpus, mesal. 645. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 625, 626, 630, 633, 634, 638, 639, 643, 1.0 mm.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tibia, 2.7 mm; metatarsus, 1.7 mm; tarsus, 0.8 mm. Second patella and tibia, 2.5 mm; third, 1.6 mm. Fourth femur, 3.3 mm; patella and tibia, 2.7 mm; metatarsus, 1.9 mm; tarsus, 0.9 mm.

Male. Carapace with light brown band from eye region to posterior margin, narrow behind. Sternum yellow-brown. Legs orange-brown with posterior and anterior longitudinal black stripes. Dorsum of abdomen yellow-brown with a gray band on each side extending almost to posterior end; sides black; venter whitish brown except for black ring around spinnerets and dark brown book-lung covers. Abdomen rectangular, twice as long as wide (Fig. 630). Total length, 4.7 mm. Carapace, 2.1 mm long, 1.5 mm wide. First femur, 1.4 mm; patella and tibia, 1.5 mm; metatarsus, 1.0 mm; tarsus, 0.7 mm. Second patella and tibia, 1.4 mm; third, 0.7 mm. Fourth femur, 1.5 mm; patella and tibia, 1.4 mm; metatarsus, 1.0 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 6.1 to 8.0 mm, males from 3.7 to 4.7 mm. The larger specimens from Argentina may lack the black line on the femora.

Note. Males and females are rarely collected together, but both are the only representatives of the *militaris* group in southern Brazil and Argentina. In the MNHN is a male from Teresópolis, with ten females of *M. furcata.*

Diagnosis. Micrathena furcata females can be separated from other species of this group by the color markings: longitudinal dark marks on the carapace (Fig. 626), and the longitudinal black marks on the femora. Dark females can be separated by the subequal length of third and fourth spines (Figs. 625, 626).

The long, S-shaped embolus of the male is diagnostic (Fig. 631).

Distribution. Southeastern Brazil to Argentina (Map 10).

Records. BRAZIL: *Est. Espírito Santo.* Chaves, Santa Leopoldina, ♀ (MZSP); Castelo, ♂ (AMNH). *Rio de Janeiro.* Rio de Janeiro, ♀ (ZMB); Teresópolis, 10♀, ♂ (MNHN). *São Paulo.* Itapeva, 2♀ (MCZ); Jundiaí, ♀, 3♂ (MCZ, MZSP); São Paulo, 2 ♀ (IBSP); Ipiranga, 11♀ (BMNH); Serra de Bocaina, ♀ (MZSP); Osascu, ♀ (MZSP); Alto da Serra, ♀ (MZSP); Guaianazes, ♀ (MZSP); Barueri, 2♀ (MZSP); Mogi das Cruzes, ♀ (MZSP); Boracéia, imm. (MZSP); Guarulhos, ♀ (MZSP); Serra da Bocaina, ♀ (MZSP). *Paraná.* Guarapuava (Rio Coutinho), ♀ (MZSP); 65 km NE Curitiba, 2♀ (CAS); Curitiba, 5♀ (MZSP); Araucária, 10♀ (MZSP). *Santa Catarina.* Pinhal, 4♀ (EPC); Município de Monte Castelo, ♀ (MZSP). *Rio Grande do Sul.* Montenegro, 2♂ (FZRS); Tres Coroas, ♂ (FZRS); Vacaria, 19♀, 2♂ (FZRS); Triunfo, ♀, 2♂ (FZRS); Torres, ♂ (FZRS); Camaguã, ♀ (MZSP). URUGUAY: ♀ (BMNH). *Dept. Canelones.* Santa Lucía, 7♀ (IIBM). *Lavalleja.* Sección 11a, ♀ (IIBM). *San José.* Barra de Santa Lucía, imm. (IIBM). ARGENTINA: *Prov. Misiones.* Monteagudo, imm. (MACN). *Corrientes.* Esquina, ♀ (ZMK); Ibéra, 6♀ (MULP). *Entre Ríos.* Las Talas, 18♀ (MULP); Concordia, ♀ (MNRJ); San José, ♀ (MACN). *Chaco.* Manantiales, 15♀ (MULP). *Santa Fé.* Santa Fé, ♂ (MACN); Garay, 7♀ (MACN). *Tucumán.* Lules, 2♀ (IMLT); Mercedes, Famailla, 9♀ (IMLT); El Manantial, ♀ (IMLT). *Buenos Aires.* Tigre, ♀ (CUC, MACN, MULP); Buenos Aires, 5♀ (MNHN, MACN); Punta Lara, 3♀ (MULP); Paraná de los Palmas y Canal, 9♀, ♂ (MEG, MACN); Las Florida, ♀ (MACN); Delta del Paraná, 16♀ (MACN); Glew, 2♀ (MACN); Río Santiago Palo Blanco, 7♀ (MACN); Río Santiago, 7♀ (MULP); La Plata, 2♀ (MULP).

Micrathena hamifera Simon
Figures 633–637; Map 10

Micrathena hamifera Simon, 1897b: 466. Nine female syntypes from Moyobamba [San Marfin], Peru (no. 10519, MNHN), examined. Reimoser, 1917: 144. Roewer, 1942: 959. Bonnet, 1957: 2870.

Description. Female. Carapace, sternum, legs dark brown. Dorsum of abdomen with white areas, dark brown to black spines, and sclerites dark brownish black; venter whitish with dark brown sclerites, epigastric region and ring around spin-

nerets. Carapace low with narrow rim and circular thoracic depression. Abdomen trapezoidal, with eight spines: two large overhanging carapace, a smaller one on each side, a pair of heavy large spines, and two posterior (Figs. 633, 634). Total length, 9.0 mm. Carapace, 3.5 mm long, 3.0 mm wide. First femur, 2.9 mm; patella and tibia, 3.1 mm; metatarsus, 1.8 mm; tarsus, 0.8 mm. Second patella and tibia, 2.9 mm; third, 1.7 mm. Fourth femur, 3.7 mm; patella and tibia, 3.0 mm; metatarsus, 1.9 mm; tarsus, 0.9 mm.

Variation. Females vary in total length from 8.4 to 9.5 mm.

Note. The male is not known.

Diagnosis. Females are separated from others having a similar epigynum by the heavy spines of the abdomen and the relatively large carapace (Figs. 633, 634).

Distribution. Amazon region (Map 10).

Records. FRENCH GUIANA: Cayenne, imm. (K. Jelski, PAN); St. Laurent de Maroni, imm. (K. Jelski, PAN). ECUADOR: *Prov. Napo.* Coca, Napo River, May 1965 (L. Peña, MCZ); Archidona, April 1935, ♀ (Y. Mexia, CAS). *Morona-Santiago.* nr. General Plaza, 1977–1978 (N. Engler, MCZ). PERU: *Dept. San Martín.* 30 km SE of Moyobamba, June 1947, ♀, 30 km NE Moyobamba, Aug. 1947, ♀ (F. Woytkowski, AMNH). *Ucayali.* Boquerón, Aug. 1946, ♀ (F. Woytkowski, AMNH). *Huánuco.* Tingo María, 8 Oct. 1946, 2♀ (J. C. Pallister, AMNH), 15, 28 Oct., 23 Nov. 1954, 3♀ (E. I. Schlinger, E. S. Ross, CAS). BRAZIL: *Terr. Amapá.* 4 Aug. 1961, ♀ (A. Cordeiro, FZRS).

Micrathena swainsoni (Perty)
Figures 638–645; Map 10

Acrosoma swainsonii Perty, 1833: 194, pl. 38, fig. 10, ♀. Female specimen from Piauí State, Brazil (ZSM), destroyed in the last war. C. L. Koch, 1839: 121, fig. 519.

Micrathena prudens Simon, 1895: 860. Two female, one male syntypes from Asunción, Paraguay (no. 1446, MNHN), examined.

Micrathena swainsoni:—Reimoser, 1917: 99, pl. 3, fig. 6, ♀. Roewer, 1942: 964. Bonnet, 1957: 2880. Chickering, 1960c: 87, figs. 83–90, ♀, ♂.

Micrathena paraguayensis Mello-Leitão, 1931: 95. Female holotype from Paraguay (MNBA), not examined. Synonymized by Mello-Leitão, 1932.

Micrathena silvicola Badcock, 1932: 27, fig. 19, ♀, ♂. Female, male syntypes from Makthlawaiya, Paraguay (BMNH), examined. Synonymized by Chickering, 1960c.

Description. Female from Paraguay. Carapace, sternum, legs brown. Dorsum of abdomen black and white, with spines black; sides black with some white spots; venter black with paired white spots on sides. Eye region of carapace projecting above clypeus, with rim only seen from side and with a round thoracic mark (Figs. 638, 639). Abdomen longer than wide, with eight spines (Figs. 638, 639). Total length, 11.0 mm. Carapace, 3.6 mm long, 2.0 mm wide. First femur, 2.9 mm; patella and tibia, 3.2 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm. Second patella and tibia, 2.8 mm; third, 1.9 mm. Fourth femur, 4.1 mm; patella and tibia, 3.0 mm; metatarsus, 2.4 mm; tarsus, 1.0 mm.

Male. Carapace orange-brown, sternum orange with some gray. Legs orange-brown with distal articles much darker. Dorsum of abdomen orange with black spines and a white spot on each anterolateral corner; sides and venter gray. Carapace oval, elongate, without rims or dimples, and with tiny teeth on the edge; thoracic depression indistinct and eyes overhanging as in female. No coxal hook. Abdomen with four pairs of spines (Fig. 643). Total length, 8.4 mm. Carapace, 3.4 mm long, 1.7 mm wide. First femur, 2.7 mm; patella and tibia, 3.0 mm; metatarsus, 2.3 mm; tarsus, 0.9 mm. Second patella and tibia, 2.7 mm; third, 1.9 mm. Fourth femur, 3.4 mm; patella and tibia, 3.1 mm; metatarsus, 2.4 mm; tarsus, 0.9 mm.

Variation. Females vary in total length from 7.3 to 11.0 mm, males from 7.7 to 9.1 mm.

Note. Males are often collected with females and have an abdomen resembling that of females.

Diagnosis. Unlike all other *Micrathena*, the abdomen is rectangular, two to

three times as long as wide, with eight black spines in both sexes (Figs. 639, 643). The epigynum has a transverse bulge, dark near its edge (Figs. 640–642). The palpus has a large curved embolus curled around the top of the bulb (Fig. 644).

Natural History. Badcock (1932) reports the species from woods; one collection from near Piraçununga, Est. São Paulo is from scrub, collected with a similar sized and colored ant. It also has been collected stored in wasp nests.

Distribution. Southern Brazil to Argentina (Map 10).

Records. BRAZIL: *Est. São Paulo.* Itapeva, 4 imm. (MCZ); Piraçununga, ♂ (MCZ, MZSP); Americana, imm. (MZSP); Rio Claro, ♀ (MZSP); Sorocaba, ♀ (MZSP); Mirassol, ♀ (MZSP); Cajuru, ♀ (MZSP); Nova Europa, ♀ (MZSP); Tabatinga, ♀ (MZSP); Miraestrela. PARAGUAY: *Dept. Alto Paraná.* Taguararapa, 5♀, 3♂ (AMNH). *La Cordillera.* San Bernardino, 4♀ (MCZ); Piribebuy, ♀ (JAK). *Paraguarí.* Sapucaí, ♀ (MACN). *Concepción.* Territ. Foncière, 26♀, 4♂, 3 imm. (NMW). *Amabay.* P.N. Cerro Corá, ♀, ♂ (JAK). ARGENTINA: *Prov. Misiones.* Posadas, 2♀ (CUC); Iguazú, ♂ (MACN); Santa Marta, imm. (MACN); Pindapoy, imm. (MULP). *Corrientes.* Manantiales, 2♀, imm. (IMLY, MACN); Maracuyá, 2♀ (MULP); Ibéra, ♀, 4 imm. (MULP). *Formosa.* Guayculé, 2♀ (MACN). *Chaco.* Resistencia, 2♀ (MULP); Tirol, imm. (MULP); Río de Oro, 2♀, imm. (MACN). *Santa Fé.* Caraguatay, imm. (MULP). *Salta.* El Tabacal, 3♀ (MACN); Las Víboras, ♀ (IMLT). *Tucumán.* Tucumán, 1 imm. (MCZ). *Buenos Aires.* Punta Lara, 4♀ (MULP).

The spinosa Group

The *spinosa* group is characterized by the female having a posteriorly biforked abdomen with two to three pairs of dorsal spines (Figs. 646, 647, 683, 684). If two pairs are present in the adult, the missing middle pair is usually replaced by scars (Fig. 647). There are no spines overhanging the carapace or on the underside of the abdomen. The females of all species are similar to each other. The epigynum is a bulge with an anterior pair of grooves or pockets in many species; the openings are posterior (Figs. 677–679). The carapace has an indistinct transverse groove behind the head and, seen in dorsal view, a rim and a distinct thoracic depression (Figs. 654, 655). The sternum is sculptured (Fig. 726). All species have the carapace, sternum and distal articles of legs dark; the coxae are often lighter than the sternum. The abdomen has paired light yellow-white patches on the dorsum, small ones on the venter [except in *M. coca*, which has two or three large light patches on black on the underside (Fig. 725)]. The forks of the abdomen are orange to black, the spines black.

Males have a trapezoidal abdomen, widest behind, in some cases with straight sides (*coca*, Fig. 709; *sexspinosa*, Fig. 717) with spines (*donaldi*, Fig. 688), or bulging (*anchicaya*, Fig. 759; *spinosa*, Fig. 701). The carapace of males is glossy, widest usually in the anterior half, with a distinct round thoracic depression. All lack a hook on the first coxa and the corresponding groove on the second femur. The palpus has a straight to slightly curved embolus with a large terminal apophysis, a median apophysis bearing a characteristic finger (Figs. 673, 681), and a complex conductor which does not hold the embolus. The palpal tibia is ventrally modified with a distal ridge (Figs. 652, 681) (which separates this species group from the *gracilis* group). In most species the embolus and terminal apophysis break off when mating and plug the epigynal opening (Figs. 727–730), making a second mating more difficult for females and impossible for males. Sometimes, however, there are two sets of palpal parts on the same side in *M. sexspinosa*. Since males lacking embolus and terminal apophysis were not among collections, it is assumed that males do not survive mating. While Figures 729–730 show the terminal apophysis and embolus as found in epigyna, only a part of the

terminal apophysis appears to break off in *M. coca* (Fig. 729) and *M. donaldi* (Fig. 727). The "wing" protruding from the epigynal opening of *M. donaldi* is near the base of the embolus, in the palpus, hidden by the cymbium in Figure 689.

Because of similarities in the epigynum, the shape of the carapace, the extended palpal tibia, and the lack of stridulating structure on book-lungs, this group is close to the *M. militaris* group and might be considered a subgroup comprising similar species.

Diagnostic features for females are the sculpturing of the epigynum as seen in ventral, posterior and lateral views, and the thickness and length of the abdominal forks and spines. The shape of the embolus and terminal apophysis stuck in the epigynum is diagnostic (Figs. 727–730). Males can be separated by the shape of the paracymbium (Fig. 719), the terminal apophysis and conductor of the palpus (Fig. 731). Males are much easier to determine than females. Juvenile (? females) of all species have six dorsal spines (Figs. 720, 721), adults except *M. donaldi* only four; the last spine may be as large in early instars as the forks of the abdomen.

There is the possibility that *M. anchicaya* is a subspecies of *M. sexspinosa*, and *M. coca* a subspecies of *M. spinosa*. The few males in collections make a decision difficult.

KEY TO THE *SPINOSA* GROUP

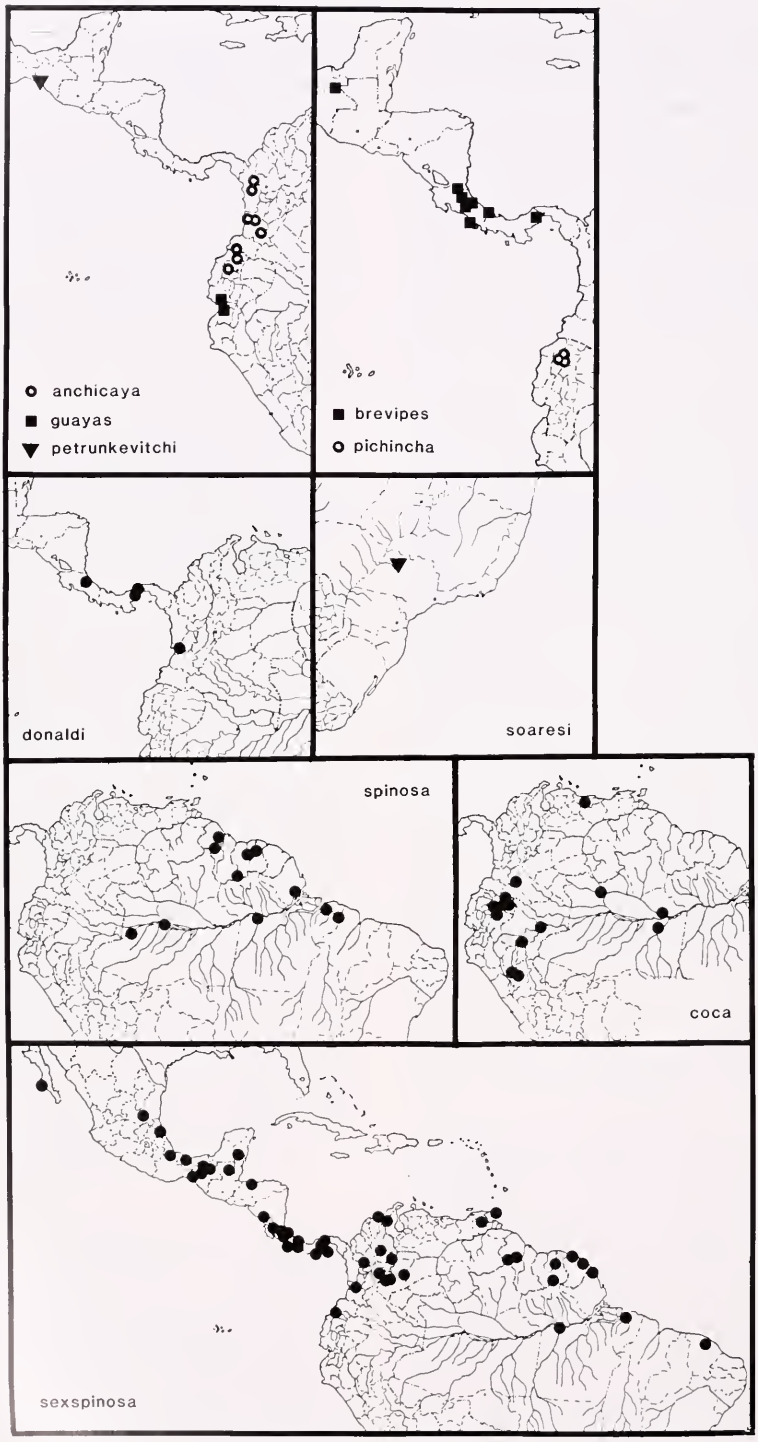
Females

1. Epigynum in ventral view with a pair of pockets or grooves on the anterior slope of bulge (Figs. 677, 685) 5
– Epigynum in ventral view with anterior slope of bulge smooth or bulge reduced (Figs. 648, 656, 664, 714) 2
2(1) Median posterior lobe of epigynum reduced (Figs. 664, 666); Chiapas, Map 11 ..... *petrunkevitchi*
– Median posterior lobe of epigynum present (Figs. 648, 656) 3
3(2) In profile median lobe with a hole (Fig. 716) or groove (Fig. 658) 4
– In profile median lobe lacking hole or groove (Fig. 650); western Ecuador, Map 11 ..... *guayas*
4(3) Median lobe wider than long in ventral view, wider than lateral depressions (Fig. 656); abdomen forks short and stubby (Fig. 655); western Colombia, Ecuador, Map 11 ..... *anchicaya*
– Median lobe as wide as long in ventral view and as wide as lateral depressions (Fig. 714); abdomen forks moderately long (Fig. 713); Mexico to Ecuador and northeastern Brazil, Map 11 ..... *sexspinosa*
5(1) Epigynum with median septum in posterior view (Fig. 686); abdomen with 6 spines (Figs. 683, 684); Costa Rica to Colombia, Map 11 ..... *donaldi*
– Epigynum with a transverse swelling in posterior view (Figs. 670, 678, 694, 699, 707); abdomen usually with only four spines in adult or, if six spines, the second pair is small (Figs. 667, 675, 697) 6
6(5) Abdomen forks as long as abdomen without them (Fig. 676); first pair of spines much longer than second (Fig. 675); epigynum as in Figs. 677–679; Chiapas to Panama, Map 11 ..... *brevipes*
– Abdomen forks shorter (Fig. 705); spines of two pairs subequal in size (Fig. 704); epigynum otherwise 7
7(6) Venter of abdomen with two or three large light patches (Fig. 725); epigynum as in Figs. 706–708; Venezuela and Amazon area, Map 11 ..... *coca*
– Venter with only small light patches; epigynum otherwise (Figs. 722, 724) 8
8(7) Epigynum with a small median lobe flanked by grooves on each side and a transverse swelling behind (Fig. 669); north-central Ecuador, Map 11 ..... *pichincha*
– Epigynum with a large median lobe (Figs. 693, 698) 9
9(8) Median lobe as wide as length of grooves on each side (Fig. 698); in posterior view a pair of depressions dorsally (Fig. 699); Guianas, Brazilian Amazon, Map 11 ..... *spinosa*
– Median lobe narrower than length of grooves on each side (Fig. 693); in posterior vew only slits present (Fig. 694); southeastern Brazil, Map 11 ..... *soaresi*

Males

The males of *M. petrunkevitchi* and *M. soaresi* are unknown.

1. Ventral and dorsal lobes of paracymbium subequal in size (Figs. 674, 682) 2
– Ventral lobe (left in Figs. 653, 661, 731) smaller than dorsal lobe of paracymbium (Figs. 653, 661, 690, 731) 3
2(1) Tip of terminal apophysis bird-head-shaped



Map 11. Distribution of *Micrathena* species of the *spinosa* group.

(Fig. 681); terminal apophysis and conductor extending beyond the tegulum (Fig. 681); Chiapas to Panama, Map 11 ..... *brevipes*

– Tip of terminal apophysis not sclerotized; terminal apophyis and conductor framed by tegulum (Fig. 673); north-central Ecuador, Map 11 ..... *pichincha*

3(1) Abdomen with indistinct spines (Fig. 688); dorsal lobe of paracymbium a hook (Fig. 690); finger of median apophysis recurved (Fig. 689); Costa Rica to Colombia, Map 11 ..... *donaldi*

– Abdomen without spines (Figs. 651, 659, 701); paracymbium and median apophysis otherwise 4

4(3) Length of paracymbium equals height of bulb (Figs. 711, 719) 5

– Length of paracymbium much shorter, about equal to half height of bulb (Figs. 653, 661, 703) 6

5(4) Paracymbium flat (Fig. 711); Venezuela and Amazon area, Map 11 ..... *coca*

– Paracymbium tubular (Fig. 719); Mexico to Ecuador and northeastern Brazil, Map 11 ..... *sexspinosa*

6(4) Paracymbium with a dorsal lobe (right in Figs. 653, 703) 7

– Paracymbium without dorsal lobe (Fig. 661); western Colombia, Ecuador, Map 11 ..... *anchicaya*

7(6) Dorsal lobe of paracymbium about as long as curved tip (Fig. 653); western Ecuador, Map 11 ..... *guayas*

– Dorsal lobe of paracymbium longer than curved tip (Fig. 703); Guianas, Brazilian Amazon, Map 11 ..... *spinosa*

Micrathena guayas new species
Figures 646–653; Map 11

Holotype. Female from Guayaquil, Guayas, Ecuador, 4 March 1983 (R. G. Schuster, CAS). The specimen is named after the Ecuadorian Province as a noun in apposition.

Description. Female. Head, thorax dark brown, sides between head and thorax lighter orange (Fig. 647). Sternum dark brown, orange posteriorly. Coxae light orange, distal leg articles orange. Posterior median eyes 1.3 diameters of other eyes. Anterior median eyes slightly more than their diameter apart; posterior median eyes 1.5 diameters apart. Two posterior forks of the abdomen short and stout (Fig. 647). Total length, 8.5 mm. Carapace, 3.2 mm long, 2.4 mm wide. First femur, 3.0 mm; patella and tibia, 3.0 mm; metatarsus, 2.0 mm; tarsus, 1.3 mm. Second patella and tibia, 2.7 mm; third, 1.7 mm. Fourth femur, 4.2 mm; patella and tibia, 3.2 mm; metatarsus, 2.4 mm; tarsus, 1.1 mm.

Male. Carapace shiny brown, sternum orange to brown, patchy. Legs brown. Dorsum of abdomen brown with three white spots, margin orange. Venter with black pigment. Abdomen trapezoid with sides wavy (Fig. 651). Total length, 5.8 mm. Carapace, 2.2 mm long, 1.4 mm wide. First femur, 1.4 mm; patella and tibia, 1.7 mm; metatarsus, 0.9 mm; tarsus, 0.6 mm. Second patella and tibia, 1.4 mm; third, 0.8 mm. Fourth femur, 2.1 mm; patella and tibia, 1.7 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm.

Note. The male which might belong with the female comes from "Palmal—Peru/Ecuador" [probably Palmales, Prov. El Oro, Ecuador].

Diagnosis. Like *M. anchicaya*, this species has very short abdominal forks (Fig. 647). Females differ in having the posterior median lobe of the epigynum quite flat and indistinct (Fig. 648); in posterior view the sides overhang the short, light median septum (Fig. 649).

The male differs from *M. spinosa* by having a narrower terminal apophysis (Fig. 652), and the paracymbium with a dorsal lobe and hook (Fig. 653).

Distribution. Western Ecuador (Map 11).

Paratypes. ECUADOR: *Prov. El Oro.* Palmales, ♂ (K. Jelski, J. Sztolcman, PAN).

Micrathena anchicaya new species
Figures 654–661; Map 11

Holotype. Female from Río Anchicayá, 400 m, Dept. Valle, Colombia (W. Eberhard, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace dark brown, head black, sides of thorax lightest. Abdomen with both posterior forks short (Fig. 655). Total length, 7.6 mm. Carapace, 3.0 mm long, 2.2 mm wide. First femur, 2.9 mm; patella and tibia, 2.9

mm; metatarsus, 1.9 mm; tarsus, 0.9 mm. Second patella and tibia, 2.7 mm; third, 1.7 mm. Fourth femur, 3.6 mm; patella and tibia, 3.3 mm; metatarsus, 2.1 mm; tarsus, 0.9 mm.

Male. Carapace dark brown. Legs, sternum orange. Dorsum of abdomen brown with lateral black spots and median white patches (Fig. 659). Venter gray, sclerotized areas brown. Carapace with an oval median thoracic depression. Abdomen trapezoidal (Fig. 659). Total length, 3.9 mm. Carapace, 1.7 mm long, 1.1 mm wide. First femur, 1.2 mm; patella and tibia, 1.2 mm; metatarsus, 0.7 mm; tarsus, 0.4 mm. Second patella and tibia, 1.1 mm; third, 0.6 mm. Fourth femur, 1.4 mm; patella and tibia, 1.2 mm; metatarsus, 0.8 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 7.5 to 8.5 mm, males from 3.9 to 4.2 mm.

Notes. Males and females were matched because of finding two males within the distribution range of females, and one from the type locality. The epigyna do not contain broken palpal pieces.

Diagnosis. Females of *M. anchicaya* differ from *M. sexspinosa* by having shorter posterior forks of the abdomen (Fig. 655), by being smaller in size and by having a wider median bulge of the epigynum (Fig. 656). Males differ by having the paracymbium curved (Fig. 661) and the knob of the paracymbium toward the bulb on a stalk (not shown in illustration).

Distribution. Western Colombia, Ecuador (Map 11).

Paratypes. COLOMBIA: *Dept. Antioquia.* Río Atrato Valley, 1,000 m, 18 March 1958, 5♀ (W. Weyrauch, EPC). *Choco.* Río Atrato Valley nr. Quibdo, 18 Jan. 1958, 3♀ (W. Weyrauch, IMLT). *Valle.* Anchicaya, 400 m, 1978, 2♀, 1977, 2♂ (W. Eberhard, MCZ); Lago Calima, 1,300 m, April 1976, ♀ (W. Eberhard, MCZ); Queremal, 12 Feb. 1976, ♂ (W. Eberhard, MCZ); Queremal to Buenaventura, 17 Feb. 1935, ♀ (H. F. Schwarz, AMNH); 28 km E of Buenaventura, 20 Jan. 1970, ♀, July 1973, ♀ (W. Eberhard, MCZ); near Puerto Patina, 10–13 July 1981, ♀ (B. Opell, MCZ); Río Jumundi, 1,000 m, ♀ (W. Eberhard, MCZ). *Cauca.* Silvia, Aug. 1975, ♀ (W. Eberhard, MCZ). *Nariño.* Barbacoas, 20 m el., 20 March 1974, 2♀ (W. Eberhard, MCZ). ECUADOR: *Pichincha Prov.* 10 km W Santo Domingo, 23 Feb. 1955, ♀ (E. I. Schlinger, E. S. Ross, CAS). *Imbabura.* Hacienda Paramba [0°49′N:78°21′W], May 1898, 3♀ (Rosenberg, BMNH).

Micrathena petrunkevitchi new species
Figures 662–666; Map 11

Holotype. Female and one female paratype from Tonala, Chiapas, Mexico, August 1909 (A. Petrunkevitch, AMNH). The species is named after its collector, the well known arachnologist.

Description. Female. Carapace blackish brown with orange rim. Sternum blackish brown. Coxae and legs brown. Carapace with a median and transverse groove and several posterior longitudinal grooves. Abdomen forks swollen (Fig. 663). Total length, 10.0 mm. Carapace, 4.3 mm long, 3.0 mm wide. First femur, 4.4 mm; patella and tibia, 4.2 mm; metatarsus, 3.0 mm; tarsus, 1.2 mm. Second patella and tibia, 3.9 mm; third, 2.3 mm. Fourth femur, 5.7 mm; patella and tibia, 4.6 mm; metatarsus, 3.3 mm; tarsus, 1.2 mm.

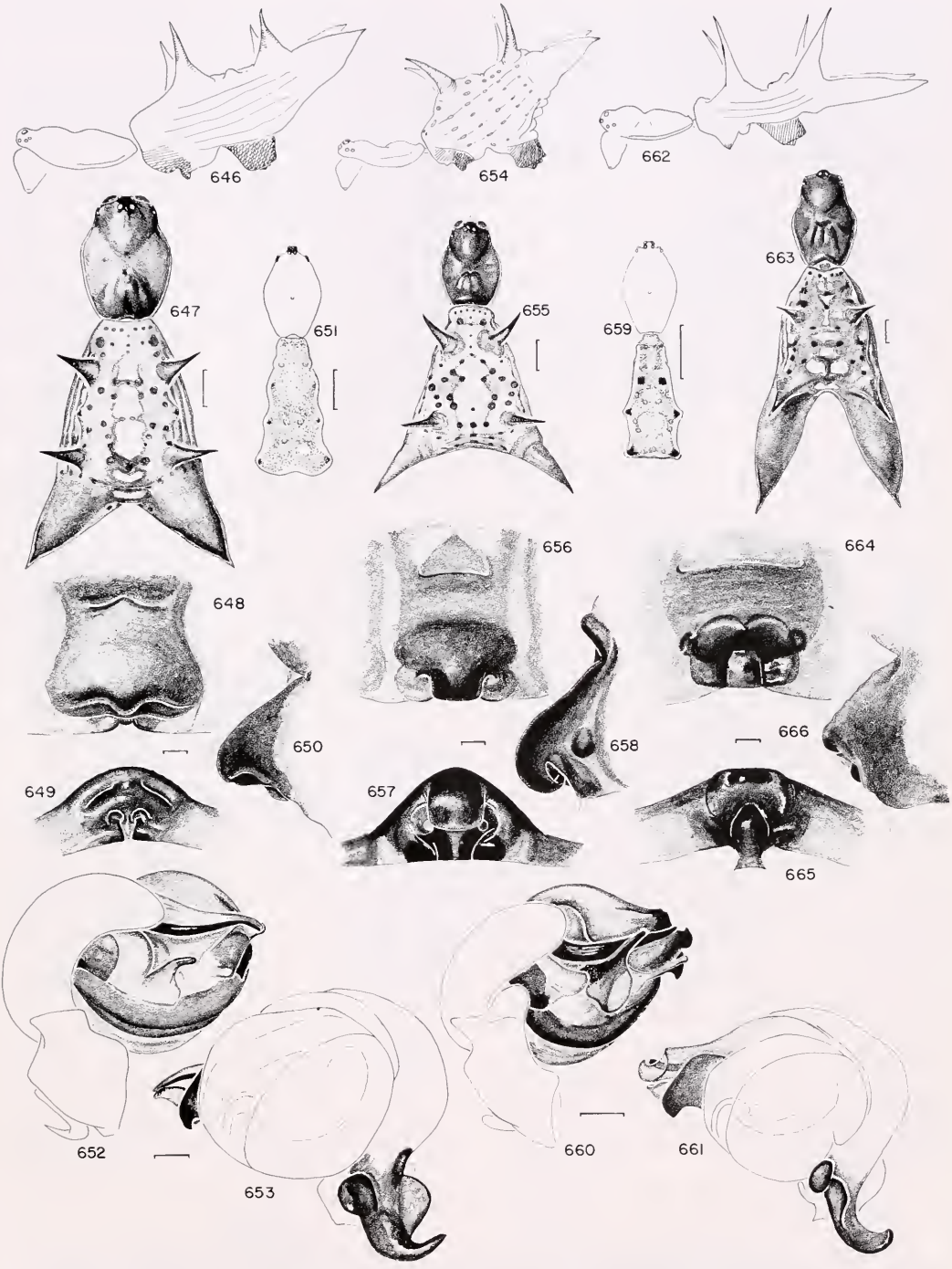
Note. Both females are in poor condition as a result of having been kept in a cork-stoppered vial for seventy years. Petrunkevitch considered the specimens to be *M. obtusispinosa.*

Diagnosis. The epigynum distinguishes

→

Figures 646–653. *Micrathena guayas* n. sp. 646–650. Female. 646. Lateral. 647. Dorsal. 648. Epigynum, ventral. 649. Epigynum, posterior. 650. Epigynum, lateral. 651–653. Male. 651. Dorsal. 652. Left palpus, mesal. 653. Palpus, lateral.

Figures 654–661. *Micrathena anchicaya* n. sp. 654–658. Female. 654. Lateral. 655. Dorsal. 656. Epigynum, ventral. 657. Epigynum, posterior. 658. Epigynum, lateral. 659–661. Male. 659. Dorsal. 660. Palpus, mesal. 661. Palpus, lateral.



Figures 662–666. *Micrathena petrunkevitchi* n. sp., female. 662. Lateral. 663. Dorsal. 664. Epigynum, ventral. 665. Epigynum, posterior. 666. Epigynum, lateral.

Scale lines. 0.1 mm, except Figures 646, 647, 651, 654, 655, 659, 662, 663, 1.0 mm.

this species from all others of the *M. sexspinosa* group. It lacks pockets on the anterior slope of the bulge and lacks the median lobe of the bulge overhanging the posterior (Figs. 664–666). The openings are probably in the slits to the side of the posterior plate.

Micrathena pichincha new species
Figures 667–674, 722; Map 11

Holotype. Female, and one female and one male paratype from 20 km northeast of Alluriquín, 4,000 m, 27 June 1975, Pichincha Prov., Ecuador (S. and J. Peck, MCZ). The specific name is a noun in apposition after the name of the province of the type locality.

Description. Female. Abdomen very contrastingly marked, black and white with many smaller sized light spots on venter. Forks of abdomen short and thick (Fig. 668); first pair of spines longer than the second (Fig. 667). Total length, 10.7 mm. Carapace, 3.9 mm long, 3.1 mm wide. First femur, 3.5 mm; patella and tibia, 3.5 mm; metatarsus, 2.0 mm; tarsus, 1.1 mm. Second patella and tibia, 3.2 mm; third, 2.1 mm. Fourth femur, 4.6 mm; patella and tibia 3.6 mm; metatarsus, 2.6 mm; tarsus, 1.1 mm.

Male with trapezoidal abdomen and three pairs of humps, second pair large (Fig. 672). Total length, 6.0 mm. Carapace, 2.5 mm long, 1.6 mm wide. First femur, 1.6 mm; patella and tibia, 1.7 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm. Second patella and tibia, 1.6 mm; third, 1.0 mm. Fourth femur, 2.1 mm; patella and tibia, 1.9 mm; metatarsus, 1.0 mm; tarsus, 0.6 mm.

Variation. Females vary in total length from 9.4 to 11.0 mm, males from 5.4 to 6.0 mm. One female had six spines in addition to the two forks of the abdomen.

Note. Males and females have been collected together.

Diagnosis. The female can be separated from others by the long grooves or pockets anteriorly on the epigynum, on each side of a relatively small median lobe (Fig. 669). The openings are quite far dorsal (close to the body wall) and have only a dorsal lip (Fig. 670). The male can be distinguished from other species by the ventral knob of the paracymbium being larger than the dorsal hook (Fig. 674).

Distribution. North-central Ecuador (Map 11).

Paratypes. ECUADOR: *Pichincha Prov.* Santo Domingo, 7 Aug. 1969, 7♀, 2♂, 6 imm. (P., B. Wygodzinsky, AMNH); 16 km SE of Santo Domingo, 680 m, June 1975, 3♂ (S., J. Peck, MCZ); 47 km S Santo Domingo, June 1975, 2♀ (S., J. Peck, MCZ); 2.9 km SW Tandayapa, 1,820 m, 20 Feb. 1979, ♂ (L. Burnham, MCZ); Río Pilatón, ♀ (G. W. Prescott, MCZ); Tandapi, 1,300–1,500 m, 1965, 23♀ (L. Peña, MCZ); Quito to Santo Domingo, June 1963, 20♀ (L. Peña, MCZ); Lluriquia, 104 km from Quito, 750 m, 21 April 1958, 3♀ (W. Weyrauch, EPC); km 113, vía Pto. Quito, 19 May 1984, ♀ (L. Avilés, MECN).

Micrathena brevipes (O. P.-Cambridge)
Figures 675–682, 723; Map 11

Acrosoma brevipes O. P.-Cambridge, 1890: 62, pl. 8, fig. 10, ♂. Two male syntypes from Bugaba, Panama (BMNH), examined. Keyserling, 1892: 12, pl. 1, fig. 9, ♂.

?*Acrosoma sedes* Gétaz, 1893: 105. Female from Palmares, plain of Diquís [9°N, 84°W], Costa Rica, lost. NEW SYNONYMY.

Micrathena brevipes:—F. P.-Cambridge, 1904: 531, pl. 50, fig. 8, ♂. Roewer, 1942: 955. Bonnet, 1957: 2862. Chickering, 1961: 398, figs. 6–8, ♂.

Synonymy. Acrosoma sedes may be this species or *M. sexspinosa*. In the L. Koch

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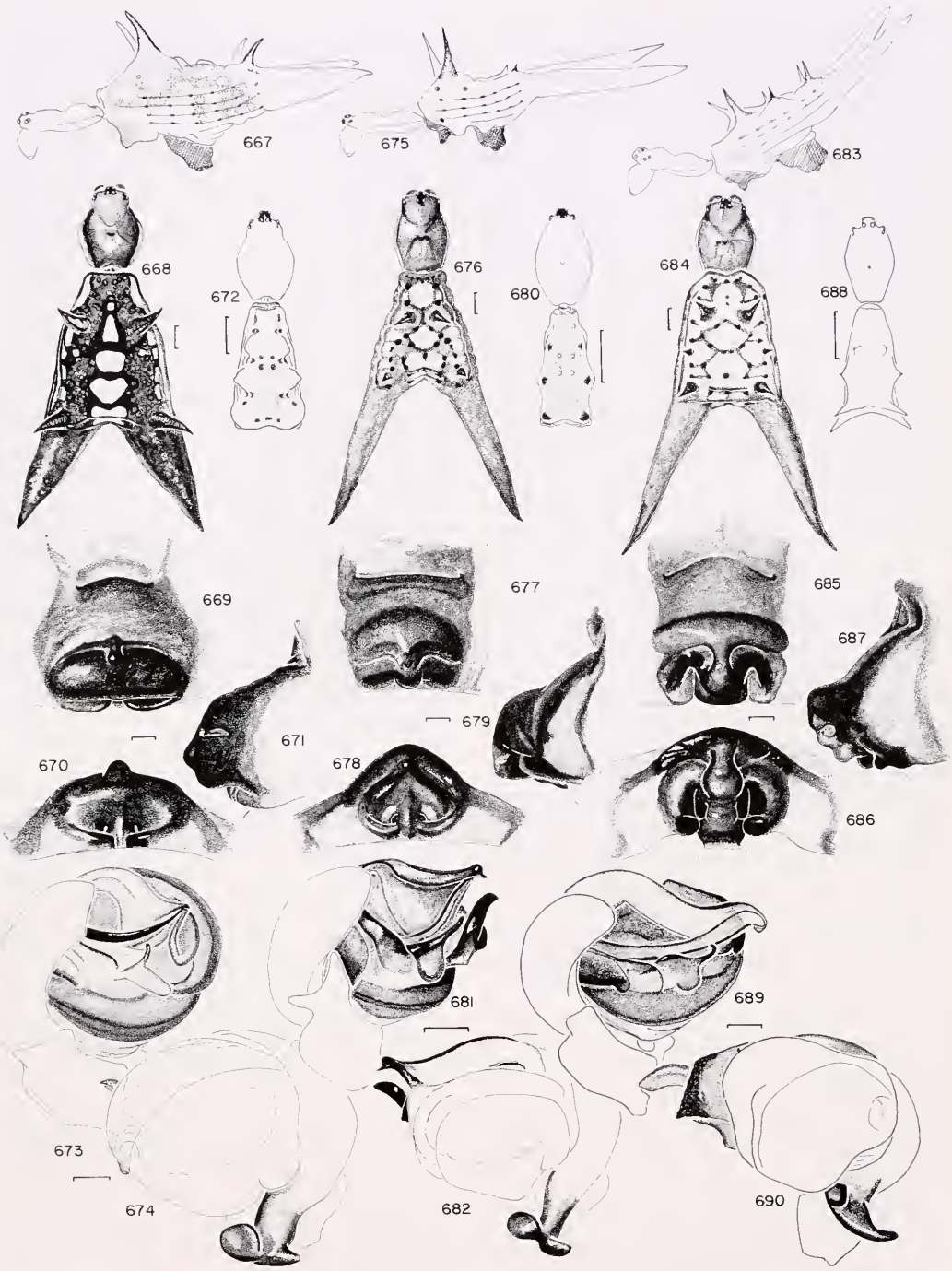
Figures 667–674. *Micrathena pichincha* n. sp. 667–671. Female. 667. Lateral. 668. Dorsal. 669. Epigynum, ventral. 670. Epigynum, posterior. 671. Epigynum, lateral. 672–674. Male. 672. Dorsal. 673. Left palpus, mesal. 674. Palpus, lateral.

Figures 675–682. *Micrathena brevipes* (O. P.-Cambridge). 675–679. Female. 675. Lateral. 676. Dorsal. 677. Epigynum, ventral. 678. Epigynum, posterior. 679. Epigynum, lateral. 680–682. Male. 680. Dorsal. 681. Palpus, mesal. 682. Palpus, lateral.



Figures 683–690. *Micrathena donaldi* Chickering. 683–687. Female. 683. Lateral. 684. Dorsal. 685. Epigynum, ventral. 686. Epigynum, posterior. 687. Epigynum, lateral. 688–690. Male. 688. Dorsal. 689. Palpus, mesal. 690. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 667, 668, 672, 675, 676, 680, 683, 684, 688, 1.0 mm.

collection (BMNH) is a specimen of *M. brevipes* labeled as *M. armata*.

Description. Female from Costa Rica. Forks of abdomen long and slender (Fig. 676); anterior spines large; tiny scars in the middle on each side, and a tooth posteriorly on each side (Fig. 675). Total length, 8.6 mm. Carapace, 3.5 mm long, 2.7 mm wide. First femur, 3.5 mm; patella and tibia, 3.4 mm; metatarsus, 2.2 mm; tarsus, 1.1 mm. Second patella and tibia, 3.3 mm; third, 2.0 mm. Fourth femur, 4.7 mm; patella and tibia, 4.0 mm; metatarsus, 2.7 mm; tarsus, 1.2 mm.

Male from La Selva, Puerto Viejo, Costa Rica. Carapace shiny dark brown. Sternum orange with white pigment at anterior and posterior ends. Legs orange with dusky longitudinal lines dorsally. Dorsum of abdomen brown with paired black patches. Abdomen slightly narrower anteriorly than posteriorly, sides almost parallel and slightly lobed (Fig. 680). Total length, 4.0 mm. Carapace, 1.8 mm long, 1.1 mm wide. First femur, 0.9 mm; patella and tibia, 1.2 mm; metatarsus, 0.6 mm; tarsus, 0.5 mm. Second patella and tibia, 1.0 mm; third, 0.7 mm. Fourth femur, 1.3 mm; patella and tibia, 1.2 mm; metatarsus, 0.8 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 7.9 to 9.9 mm, males from 4.0 to 4.3 mm.

Note. Males and females have been collected together.

Diagnosis. The female is distinguished from *M. sexspinosa* by having longer, more slender abdominal forks (Fig. 676); in posterior view the epigynum lacks a septum, unlike *M. sexspinosa* and *M. donaldi*. Instead it has a transverse swollen ridge with the openings dorsal, close to the body wall (Fig. 678), as in *M. pichincha*.

The male differs from *M. sexspinosa* and *M. donaldi* by having the two parts of the paracymbium equal in size (Fig. 682); while the dorsal part is longer in the two other species. The male differs from *M. pichincha*, which has a similar paracymbium, by having a longer embolus and terminal apophysis (Figs. 681, 682).

Natural History. Females have been found in webs in low vegetation in dense jungle and forest.

Distribution. Southern Mexico to northern Panama (Map 11).

Records. MEXICO: *Est. Chiapas.* Palenque ruins area, 2–11 July 1983, ♀ (W. Maddison, R. S. Anderson, MCZ). COSTA RICA: *Heredia Prov.* Puerto Viejo, La Selva, ♀, ♂ (many collections, MCZ). *Alajuela.* San Carlos, 25 March 1980, ♀ (MZCR). *Limón.* Siquirres, 20–23 May 1944, ♀ (F. Schrader, AMNH); Waldeck Farm, 4 Aug. 1930, 3♀, ♂ (E. Reimoser, NMW). *San José.* San José, ♀ (N. Banks, MCZ); Braulio Carillo Natl. Park, 26 July 1983, 3♀ (H. and L. Levi, W. Eberhard, MCZ), 25 Oct. 1981, 2♀ (A. Coto, MZCR); San Francisco de Dos Ríos, 10 March 1981, ♀ (C. Gomez, MZCR). *Puntarenas.* Isla Caño, 19 Feb. 1970, 2♀ (D. C. Robinson, MZCR). PANAMA: ♀ (BMNH). *Prov. Panamá.* Alturas Cerro Campana, Dist. Capira, 9 April 1977, 2♀ (A. Arauz, D. Quintero, UPMI).

Micrathena donaldi Chickering
Figures 683–690, 727; Map 11

Micrathena donaldi Chickering, 1961: 405, figs. 31–34, ♂. Male holotype from Barro Colorado Island, Gatún Lake, Panama (MCZ), examined.

Description. Female. Abdomen with three pairs of dorsal spines, median one smallest, and long, slender fork (Figs. 683, 684). Total length, 9.4 mm. Carapace, 3.7 mm long, 3.0 mm wide. First femur, 4.2 mm; patella and tibia, 4.2 mm; metatarsus, 2.7 mm; tarsus, 1.2 mm. Second patella and tibia, 3.7 mm; third, 2.3 mm. Fourth femur, 5.5 mm; patella and tibia, 4.5 mm; metatarsus, 3.0 mm; tarsus, 1.2 mm.

Male. Carapace very smooth with a median circular thoracic mark. Abdomen with four large posterior spines and four small dorsal ones (Fig. 688). Total length, 4.2 mm. Carapace, 1.8 mm long, 1.1 mm

wide. First femur, 1.3 mm; patella and tibia, 1.3 mm; metatarsus, 0.7 mm; tarsus, 0.6 mm. Second patella and tibia, 1.2 mm; third, 0.8 mm. Fourth femur, 1.9 mm; patella and tibia, 1.6 mm; metatarsus, 1.1 mm; tarsus, 0.6 mm.

Variation. Females vary in total length from 8.2 to 10.3 mm, males from 4.2 to 4.6 mm.

Note. Males and females are common on Barro Colorado Island, Gatún Lake, Panama.

Diagnosis. Females can be separated from those of *M. sexspinosa* by the more slender forks of the abdomen (Fig. 684) and by having three pairs of dorsal spines (Fig. 683), and by the epigynum having a pair of pockets on the anterior face on each side of the bulge (Fig. 685). They differ from females of *M. brevipes* in having a longitudinal septum in posterior view of the epigynum (Fig. 686). The parts of the male palpus broken off after mating extend from the epigynal openings like insect wings and are diagnostic (Fig. 727).

Males can be separated from *M. sexspinosa* by having a much shorter paracymbium (Fig. 690) and a slender, curved embolus (Fig. 689). Males differ from *M. brevipes* by having a longer dorsal part to the paracymbium (Fig. 690).

Distribution. Costa Rica to western Colombia (Map 11).

Records. COSTA RICA: *Prov. Limón.* Waldeck Farm, 4 Aug. 1930, ♀ (E. Reimoser, NMW). PANAMA: *Prov. Panamá.* Barro Colorado Island, Gatún Lake, ♀♀, ♂♂ (common, AMNH, EPC, MCZ); Capira, 11 Nov. 1979, ♀ (J. Regalado, UPMI). COLOMBIA: *Dept. Valle.* 28 km E of Buenaventura, ♀ (W. Eberhard, MCZ).

Micrathena soaresi new species
Figures 691–695, 724; Map 11

Holotype. Female from Mirassol, Est. São Paulo, Brazil, 10 June 1964 (no. 3464, MZSP). The species is named after B. M. Soares, Brazilian arachnologist.

Description. Female. Carapace orange-brown, rim whitish. Sternum dark brown; coxae, legs orange-brown. Posterior median eyes slightly larger than anteriors; anterior laterals equal; posterior laterals slightly smaller than anterior median eyes. Abdomen forked with four spines and a pair of scars in between; forks short (Figs. 691, 692). Total length, 8.9 mm. Carapace, 3.5 mm long, 2.4 mm wide. First femur, 3.2 mm; patella and tibia, 3.4 mm; metatarsus, 2.2 mm; tarsus, 1.1 mm. Second patella and tibia, 3.0 mm; third, 1.9 mm. Fourth femur, 4.3 mm; patella and tibia, 3.6 mm; metatarsus, 2.6 mm; tarsus, 1.1 mm.

Diagnosis. This species differs from *M. spinosa* and *M. pichincha* by having a flat area in posterior view of the epigynum (Fig. 694); the openings are tucked in slits dorsally and not visible in posterior view.

Micrathena spinosa (Linnaeus)
Figures 696–703, 720, 728; Map 11

Araneae spinosa Linneaus, 1758: 624. Specimen from America (not *spinosa* of most authors). Neotype here designated from Santarém, Brazil (BMNH).

Aranea aculeata Fabricius, 1775: 345. Specimen from America (BMNH), lost. NEW SYNONYMY.

Aranea elongatospinosa De Geer, 1778: 323, pl. 39, figs. 11, 12, juv. or ♀. Specimen from Suriname, lost. NEW SYNONYMY.

Micrathena perlata Simon, 1895: 852, fig. 905; 1897b: 467. Juvenile female lectotype here designated from São Paulo de Olivença [Est. Amazonas, Brazil] (no. 244, MNHN). Male paralectotype is *M. triangularispinosa*. NEW SYNONYMY.

Micrathena hamata Chickering, 1960a: 3, figs. 4–7, ♂. Male holotype and one paratype from Le Para [Belém], Brazil (MCZ), examined. NEW SYNONYMY.

Synonymy. Linnaeus supplied no figure, only a short diagnosis: "Aranea spinis dorsalis octonis, posticis duabus patentibus, abdomina subtus conico. Habitat in America." De Geer (1778) subsequently renamed it *triangularispinosa* and supplied a figure resembling Figure 472, of a spider having only six dorsal spines and two small ones posterior and below. DeGeer's figure does not fit Linnaeus' description of eight dorsal spines, the posterior two most distinct. After examining the many species of *Micrathena,* I find

that Linnaeus' description fits only immature females of the common *sexspinosa* group (Figs. 720, 721). It is much more likely that Linnaeus had specimens from the Amazon and northeastern South America than from Central American or western South America. There are two species of this group found in the Amazon and northeastern South America, one which has usually been referred to as *sexspinosa* (Chickering, 1961). Since using Linnaeus' name for *sexspinosa* would upset the stability of a name, an arbitrary decision has been made to use it for this species whose oldest certain name was *hamata* Chickering.

The synonymy of *A. aculeata* Fabricius and of *A. elongatospinosa* DeGeer is uncertain. Both belong to the *A. sexspinosa* group and are most likely this species. *Micrathena perlata* has two specimens in the same vial: a juvenile female, described by Simon, and an adult male. The juvenile has been designated lectotype and is probably this species. The male is *M. triangularispinosa.*

Description. Female. Abdomen biforked, with two pairs of spines, first pair slightly longer than second (Figs. 696, 697). Total length, 10.0 mm. Carapace, 4.2 mm long, 3.1 mm wide. First femur, 4.2 mm; patella and tibia, 4.3 mm; metatarsus, 2.8 mm; tarsus, 1.2 mm. Second patella and tibia, 4.0 mm; third, 2.6 mm. Fourth femur, 5.4 mm; patella and tibia, 4.6 mm; metatarsus, 3.2 mm; tarsus, 1.2 mm.

Male. Abdomen trapezoidal, sides undulating (Fig. 701). Total length, 4.5 mm. Carapace, 1.9 mm long, 1.1 mm wide. First femur, 1.2 mm; patella and tibia, 1.2 mm; metatarsus, 0.7 mm; tarsus, 0.4 mm. Second patella and tibia, 1.0 mm; third, 0.7 mm. Fourth femur, 1.4 mm; patella and tibia, 1.2 mm; metatarsus, 0.7 mm.

Variation. Females vary in total length from 8.8 to 11.5 mm, males from 4.5 to 4.7 mm.

Note. A male is with a collection of females from Kartabo, Guyana (CUC), from Vila Amazonas, Brazil (CAS) and from Belém (MEG). Palpal parts remaining in the epigynum are illustrated in Figure 728.

Diagnosis. Females of *M. spinosa* can be distinguished from the sympatric *M. sexspinosa* by having a pair of pockets on the bulge of the epigynum in ventral view (Fig. 698); in posterior view by having the deep opening close to the ventral body wall (Fig. 699); and by lacking the septum of *M. sexspinosa.*

The male can be separated by the distal hook of the relatively flat paracymbium (Fig. 703); that of *M. sexspinosa* is long and tubular.

Distribution. Guianas and Amazon region of Brazil (Map 11).

Records. GUYANA: ♀ (R. W. G. Hingston, BMNH); Kartabo, many collections, ♀♀, ♂♂ (CUC, AMNH); source of Kutari River, 1936, ♀ (BMNH); Moraballi Riv., Essequibo Riv., 24 km above Bartica, ♀ (BMNH). SURINAME: *Brokopondo Prov.* Browns Berg, 20 Feb. 1982, ♀ (D. Smith Trail, MCZ). *Suriname.* Republiek, June 1963 (P. H. van Doesburg, AMNH). BRAZIL: *Terr. Amapá.* Villa Amazonas, 29 May 1964, 2♀, ♂ (C. E., E. S. Ross, CAS); Macapá, June 1966, ♀ (IBSP). *Est. Pará.* Santarém, 8♀ (BMNH); Belém, ♀, ♂ (MCZ),

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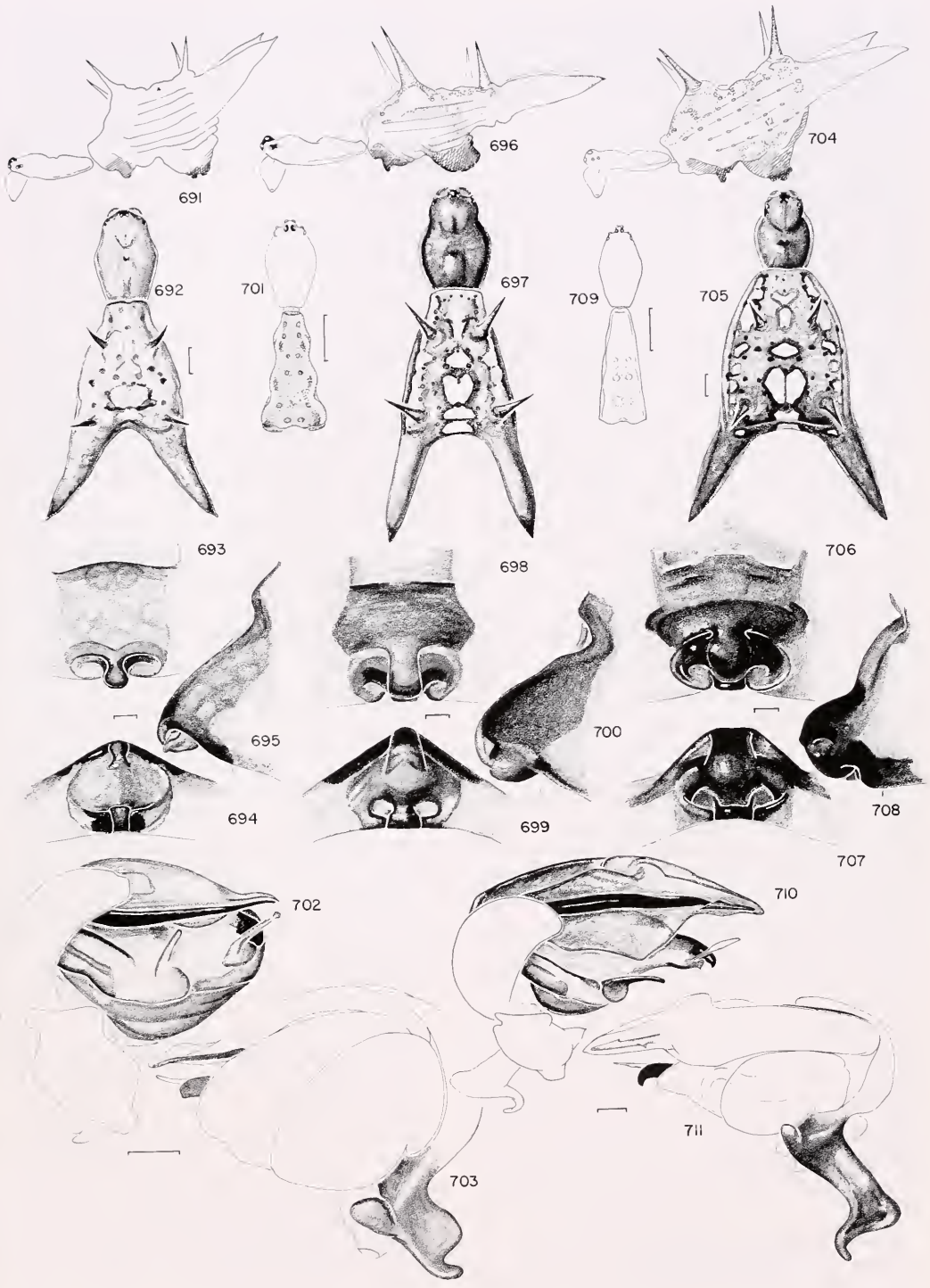
Figures 691–695. *Micrathena soaresi* n. sp., female. 691. Lateral. 692. Dorsal. 693. Epigynum, ventral. 694. Epigynum, posterior. 695. Epigynum, lateral.

Figures 696–703. *Micrathena spinosa* (Linnaeus). 696–700. Female. 696. Lateral. 697. Dorsal. 698. Epigynum, ventral. 699. Epigynum, posterior. 700. Epigynum, lateral. 701–703. Male. 701. Dorsal. 702. Left palpus, mesal. 703. Palpus, lateral.

Figures 704–711. *Micrathena coca* n. sp. 704–708. Female. 704. Lateral. 705. Dorsal. 706. Epigynum, ventral. 707. Epigynum, posterior. 708. Epigynum, lateral. 709–711. Male. 709. Dorsal. 710. Palpus, mesal. 711. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 691, 692, 696, 697, 701, 704, 705, 709, 1.0 mm.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Aug. 1971, 2♀, ♂ (M. E. Galiano, MEG), Nov. 1961, ♀ (A. R. Hoge, IBSP); Canindé, Rio Gurupi, Feb.–May 1964, ♀ (J. Carvalho, AMNH). *Amazonas.* Tefé, Nov.-Dec. 1920, 3♀ (H. S. Parish, MCZ).

Micrathena coca new species
Figures 704–711, 725, 729; Map 11

Holotype. Female from Coca, Napo River, Prov. Napo, Ecuador, May 1965 (L. Peña, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Venter of abdomen with three large white patches on black (Fig. 725). Posterior spines of abdomen as long as anterior spines (Fig. 704). Total length, 11.0 mm. Carapace, 3.9 mm long, 2.9 mm wide. First femur, 4.0 mm; patella and tibia, 3.8 mm; metatarsus, 2.5 mm; tarsus, 1.2 mm. Second patella and tibia, 3.6 mm; third, 2.2 mm. Fourth femur, 5.0 mm; patella and tibia, 4.1 mm; metatarsus, 2.7 mm; tarsus, 1.2 mm.

Male from Tingo María, Peru. Carapace brownish black, very shiny. Sternum dark brown underlain by some white pigment. Legs dark brown, first two femora darkest. Dorsum of abdomen with three white patches on brownish black; venter black. Abdomen longer than wide, narrow in front and with a posterior median notch (Fig. 709). Total length, 4.7 mm. Carapace, 2.0 mm long, 1.2 mm wide. First femur, 1.2 mm; patella and tibia, 1.2 mm; metatarsus, 0.6 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.6 mm. Fourth femur, 1.3 mm; patella and tibia, 1.2 mm; metatarsus, 0.7 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 10.9 to 11.6 mm. The white patch behind the spinnerets may be absent. In posterior view the shape of the median septum of the epigynum close to the body wall is quite variable, sometimes narrower, sometimes with the dorsal piece pointed.

Note. Males have been collected with females in Manaus, Brazil.

Diagnosis. Females of *M. coca* differ from *M. spinosa* by the pair of white patches on the underside of the abdomen (Fig. 725) and by the wider septum in posterior view of the epigynum (Fig. 707). The paracymbium of the male palpus is longer and the distal end curved in the opposite direction from that of *M. spinosa* (Fig. 711).

Natural History. Females from Limoncocha were collected in Amazonian rainforest.

Distribution. Upper Amazon area (Map 11).

Paratypes. VENEZUELA: *Prov. Aragua.* Rancho Grande, Feb. 1968, ♀ (Williner, MACN). COLOMBIA: *Dept. Coqueta.* Río Orteguaza, Aug.–Sept. 1947, 2♀ (L. Richter, AMNH). ECUADOR: *Dept. Napo.* Pompeya, Río Napo, May 1965, 2♀ (L. Peña, MCZ); Limoncocha, 240 m, 6 Feb. 1979, 2♀ (L. Burnham, MCZ). *Napo.* Tarapuy, Nov. 1982, ♀, 25 May 1984, ♀ (L. Avilés, MECN); Archidona, 21 Aug. 1964, ♀ (D. Seiwa, AMNH); Dureno, S of Río Aguarico, 150–200 m, Sept. 1977, ♀ (L. Peña, AMNH). *Pastaza.* Sarayacu, ♀ (O. C. Felton, MCZ). PERU: *Dept. Huánuco.* Aucayacu, 1 June 1967, ♀ (A. F. Archer, AMNH); Tingo María, 31 May 1967, ♂ (A. F. Archer, AMNH), Dec. 1946, 5♀ (W. Weyrauch, AMNH); Cucharas, 1954, 11♀ (F. W. Woytkowski, EPC). *Loreto.* Iquitos, May 1920, 4♀ (H. S. Parish, MCZ); Río Pacaya, 1912, 3♀ (BMNH). BRAZIL: *Est. Amazonas.* Jan. 1884, ♀ (NMW); São Gabriel, 4 Jan. 1924, ♀ (A. Roman, NRS); Rio Autas, Capiranga, 31 Aug. 1914, ♀ (A. Roman, NRS); Manaus, Aug. 1971, 2♀, ♂ (M. E. Galiano, MEG).

Micrathena sexspinosa (Hahn)
Plate 1; Figures 712–719, 721, 726, 730, 731; Map 11

Epeira sexspinosa Hahn, 1822: pl. 4, figs. A and a (labeled *Epeira furcata* mihi). Specimen from Suriname in Hahn's collection, lost.

Acrosoma sexspinosum:—Hahn, 1834: 18, fig. 107, ♀ (illustration labeled *A. furcata*). Specimen from Brazil in Sturm's collection, lost.

Plectana squamosa Walckenaer, 1841: 185. Specimens without locality, lost.

Acrosoma obtusospinum Keyserling, 1863: 76, pl. 2, fig. 9, ♀. Two female, two juvenile syntypes from St. Andrés [San Andres, Veracruz], Mexico (BMNH), examined.

Acrosoma petersii Taczanowski, 1872: 277, pl. 6, fig. 28. Juvenile female lectotype here designated, three juvenile paralectotypes, two last instar males from St. Laurent de Moroni, French Guiana and Uassa [Amapá, Brazil] (PAN), examined. NEW SYNONYMY.

Keyserlingia cornigera O. P.-Cambridge, 1890: 58, pl. 4, fig. 2, ♂. Male holotype from Bugaba, Panama (BMNH), examined. Synonymized by Chickering, 1960.

Acrosoma calcaratum O. P.-Cambridge, 1890: 62, pl. 8, fig. 8, ♂. Male holotype from Bugaba, Panama (BMNH), examined. Keyserling, 1892: 11, pl. 1, fig. 8, ♂.

Micrathena obtusospina:—F. P.-Cambridge, 1904: 531, pl. 50, fig. 9, ♀.

Micrathena cornigera:—F. P.-Cambridge, 1904: 532, pl. 50, fig. 10, ♂.

Micrathena sexspinosa:—Reimoser, 1917: 126, pl. 8, fig. 23, ♀. Roewer, 1942: 963. Bonnet, 1957: 2877. Chickering, 1961: 456, figs. 174–180, ♀, ♂.

Synonymy. In 1822 Hahn inverted pictures and names of *Epeira furcata* and *Epeira sexspinosa*, and again in 1834 with *Acrosoma bifurcata* and *A. sexspinosa*. In 1834 Hahn under the text heading *A. bifurcata* has "A. 6-spinosa, in Tabula" in brackets. Reimoser (1917) does not mention Hahn's confusion and illustrated (fig. 23) the species he, Chickering and I consider *sexspinosa*. Bonnet (1957: 2862) mentions the inversion in a footnote.

I follow here previous revisers (Reimoser, 1917; Chickering, 1961) in considering *obtusospina* a synonym of *sexspinosa*, although Hahn's figure could be *M. spinosa* (Linn.).

Some synonyms, names based on juvenile types, are to some extent arbitrary: *petersii* from French Guiana could be *spinosa*. *Keyserlingia cornigera* and *Acrosoma calcaratum* are males of this species.

The name *sexspinosa* has been used in the literature for females of all members of this species group.

Description. Female from Panama. Abdomen with two pairs of slender dorsal spines; rarely a smaller spine in between (Figs. 712, 713). Total length, 11.0 mm. Carapace, 3.8 mm long, 2.7 mm wide. First femur, 4.0 mm; patella and tibia, 3.7 mm; metatarsus, 2.5 mm; tarsus, 1.2 mm. Second patella and tibia, 3.5 mm; third, 2.2 mm. Fourth femur, 5.3 mm; patella and tibia, 4.0 mm; metatarsus, 3.1 mm; tarsus, 1.2 mm.

Male from Panama. Abdomen trapezoidal, with two posterolateral lobes (Fig. 717). Total length, 5.2 mm. Carapace, 2.1 mm long, 1.9 mm wide. First femur, 1.4 mm; patella and tibia, 1.3 mm; metatarsus, 0.7 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.8 mm. Fourth femur, 1.6 mm; patella and tibia, 1.3 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 7.7 to 11.8 mm, males from 4.5 to 5.2 mm. Both spines and forks are extremely variable and often resemble in each region the spination of the endemic species of this group.

Note. Males and females were first associated by Chickering (1961) and have been collected together in Mexico, Panama and Colombia. The terminal apophysis and embolus of the male palpus (Fig. 731) match the structure found in the female epigynum (Fig. 730).

Diagnosis. Females can be differentiated from other members of this species group by the lack of grooves on the anterior of the epigynal bulge (Fig. 714), by the equal diameter of the median lobe and the lateral depressions (Fig. 714), and by the median septum in posterior view (Fig. 715). The unique long, tubular paracymbium, a spur (Figs. 718, 719, 731), separates the males from all other *Micrathena* species.

Natural History. Females have been collected from "pine forest" (Chiapas), "forest trail" (Colombia) and "low vegetation in primary forest" (Costa Rica). The orange eggs are in a pale yellow egg-sac.

Distribution. Mexico to Colombia and Ceará, Brazil (Map 11).

Records. MEXICO: *Est. Baja California.* Isla Sta. Magarita, ♀ (MCZ). *San Luis Potosí.* Ciudad de Maiz, 2♀. *Veracruz.*

Poza Rica, ♀; Fortín, ♀. *Tabasco.* 2.4 km E of Teapa, ♀. *Quintana Roo.* Kohunlich ruins, 9 km S Francisco Villa, ♀. *Chiapas.* 24 km NW of Arriaga, ♀; Cerro de Madrigal, ♀, ♂; Palenque ruins, ♀, ♂; Simojovel, ♂. GUATEMALA: *El Petén.* Tikal, 3♀. HONDURAS: Lancetilla, ♀. NICARAGUA: nr. Managua, 4♀. COSTA RICA: *Prov. Heredia.* Tiribí; Puerto Viejo, 2♀. *Alajuela.* La Fortuna. *Guanacaste.* Tilarán, 3♀. *Limón.* Bomba, nr. Limón; Siquirres, 2♀; Cohuita; Waldeck Farm, ♀; Hamburg Farm, 8♀, 2♂. *Cartago.* Turrialba. *San José.* Surubres. *Puntarenas.* Golfito; Rincón de Osa, ♀; 52 km E of Palmar Sur, ♀. PANAMA: *Prov. Panamá.* common. *Boca del Toro.* Río Changuinola, nr. Quebrada El Guabo, 16 km W of Almirante. *Los Santos.* Corozal. *Coclé.* El Valle. *Chiriquí.* El Volcán, Chiriquí; David. LESSER ANTILLES: *Trinidad.* Maracas Valley, ♀; SW Navy Base, ♀, ♂; Port of Spain, ♀; Blanchisseuse, ♀; Sangre Grande, ♀. VENEZUELA: *Est. Monagas.* Caripito, ♀. GUYANA: *Bartica Distr.* Kartabo, ♀. Upper Ireng River, Pakaraima Mts., 3♀. SURINAME: Makambi Kabelstation, ♀; Brownsberg. FRENCH GUIANA: Cayenne, ♀, ♂. COLOMBIA: *Dept. Cesar.* Finca San José, Socorpa Mission, Sierra de Perija, 1,450–1,500 m, 2♀, 4♂. *Magdalena.* Minca Vall., Sierra Nevada de Santa Marta, 900 m, 5♀, 20♂. *Santander.* Río Opón, 1,000 m, ♀. *Antioquia.* Mutatá, 3♀. *Meta.* El Porvenir, ♀; Villavicencio, 500 m el., ♂; 20 km W Villavicensio, ♀; Cisneres, Río Quebrada Descansion, ♂; 15 km SW Puerto López, 200 m, ♀, ♂; Carimagua, ♂. *Boyacá.* Río Suárez, 800–1,000 m, ♀; Río Dpan, 3♀. *Cundinamarca.* Monteredondo, 1,200 m, ♀. *Valle.* Cali Distr., ♀. ECUADOR: *Prov. Esmeraldas.* Carondelet, 4♀ (BMNH). BRAZIL: *Est. Pará.* Belém, ♀ (AMNH); Santarém, 2♀ (NMW). *Ceará.* Maranguape Mts., ♀ (MCZ).

Micrathena funebris (Marx in Banks) Plate 1; Figures 732–740; Map 12

Acrosoma funebre Marx in Banks, 1898: 249. Female syntypes from Calmilla Mines and Sierra San Nicholas [Baja California] (CAS), destroyed; two syntypes from Mazatlan (MCZ), examined.

Acrosoma maculata Banks, 1900: 100. Female holotype from Arizona (MCZ), examined.

Micrathena granulata F. P.-Cambridge, 1904: 533, pl. 50, fig. 12, ♂. Male holotype from Teapa, Mexico (BMNH), examined.

Micrathena catenulata F. P.-Cambridge, 1904: 538, pl. 51, fig. 24, ♀. Three female syntypes from Sakiyac, Chamiquin, four in poor condition from Cahabon, two in poor condition from Quezaltepeque, and two females from Ayutla, Guatemala with locality labels only (BMNH), examined and labeled. Reimoser, 1917: 97. Roewer, 1942: 955. Bonnet, 1957: 2863. Chickering, 1961: 398, figs. 9–13, ♀. NEW SYNONYMY.

Micrathena funebris:—Levi, 1978: 428, figs. 28–40, ♀, ♂.

Synonymy. Specimens of *M. catenulata* were within the variation found in *M. funebris.*

Variation. Females vary in total length from 5.2 to 7.6 mm, males from 3.1 to 4.5 mm. This is a variable species. The carapace of females ranges in color from yellow to black, with or without a narrow

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Figures 712–719. *Micrathena sexspinosa* (Hahn). 712–716. Female. 712. Lateral. 713. Dorsal. 714. Epigynum, ventral. 715. Epigynum, posterior. 716. Epigynum, lateral. 717–719. Male. 717. Dorsal. 718. Left palpus, mesal. 719. Palpus, lateral.

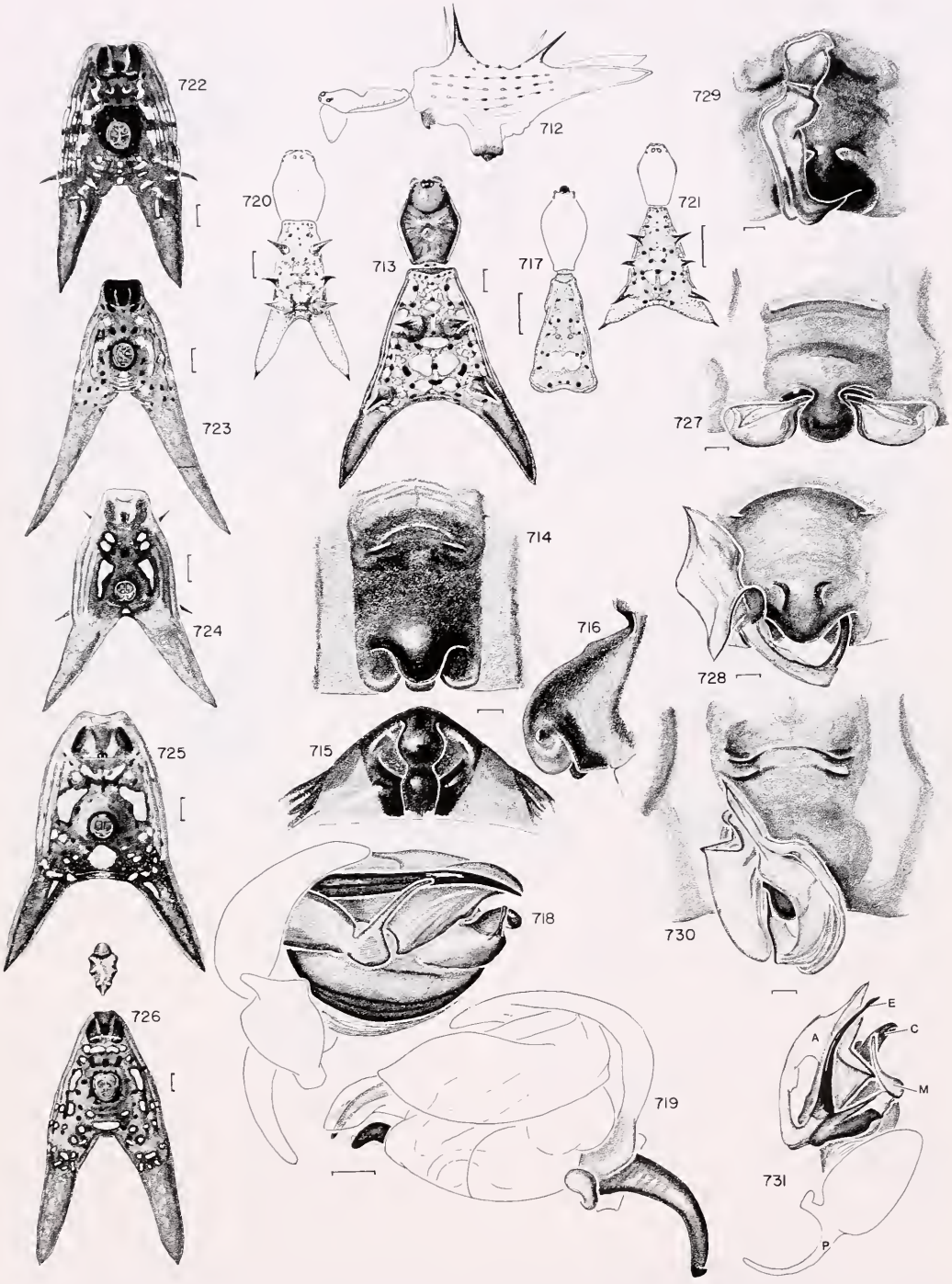
Figures 720–721. Immatures of *spinosa* group. 720. *Micrathena spinosa.* 721. *Micrathena sexspinosa.*

Figures 722–726. Venter of female abdomen. 726. Sternum and abdomen. 722. *M. pichincha.* 723. *M. brevipes.* 724. *M. soaresi.* 725. *M. coca.* 726. *M. sexspinosa.*

Figures 727–730. Epigynum plugged by terminal apophyses and emboli. 727. *M. donaldi.* 728. *M. spinosa.* 729. *M. coca.* 730. *M. sexspinosa.*

Figure 731. Expanded left palpus of *M. sexspinosa* showing embolus (E) and terminal apophysis (A). The other face, the "underside" of the left terminal apophysis and left embolus, are seen in the epigynum (Fig. 730).

Scale lines. 0.1 mm, except Figures 712, 713, 717, 720–726, 1.0 mm.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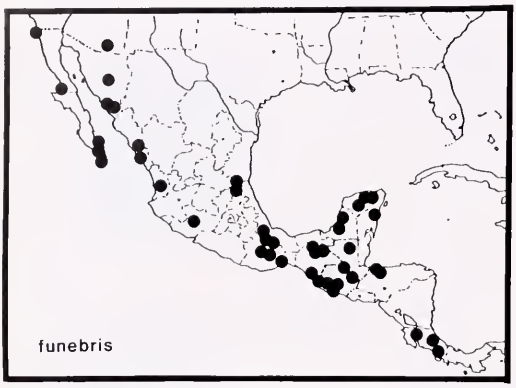

Map 12. Distribution of *Micrathena funebris*.

rim. It has from two to eight soft projections on the abdomen. If with two projections, the third pair are present; the most likely pairs to be lost are the first (the anterolaterals) and the fourth (posteroventrals). Some females have only a few black marks on the abdomen (Fig. 733), others are black, white and orange, resembling the colors of immature widow spiders *Latrodectus* (Fig. 734). The epigynum is variable in outline, but sometimes with a light patch on the anterior face (Fig. 735). Males have a variable number of macrosetae on the first femora (Fig. 738). Other illustrations are in Levi, 1978: figures 16–27.

Note. Several collections contain series of females collected with males.

Diagnosis. There are no similar species. The shape of the abdomen, longer than wide, with variable number of fleshy projections, is diagnostic, as is the bulging epigynum, whose openings are posterodorsal and always apart (Figs. 735–737).

Males have a unique median apophysis bearing a thorn and an adjacent shorter spine (Fig. 739), and a rectangular paracymbium with punctate sculpturing (Fig. 740).

Distribution. Arizona to Costa Rica (Map 12).

Records. USA: *Arizona.* Pima Co: Sabino Pond (JAB). MEXICO: *Est. Sonora.* (AMNH); Minas Nuevas (AMNH); Alamos (AMNH), 2♀ (CAS); Ciudad Obregon, ♀ (CAS). *Baja California.* 14 km SW La Paz, ♀ (EMUC); 8 km S Miraflores, ♀ (EMUC). *San Luis Potosí.* Tamazunchale (AMNH); Huichihuayan (AMNH); 5 km W El Naranjo, 2♀ (LC). *Sinaloa.* 64 km S of Culiacán (AMNH). *Nayarit.* Tepic (AMNH); La Mesa (AMNH); SE Tepic, ♀ (CAS). *Veracruz.* SE of Córdoba, ♀ (JB). *Michoacan.* 16 km S Uruapan, 2♀ (EMUC). *Oaxaca.* SE of Nejapa (AMNH); Tehuantepec (AMNH); Soyaltepec (AMNH); Temescalapa, 2♀, ♂ (MCZ); 13 km S Tuxtepec, 6♂ (MCZ). *Tabasco.* Teapa (AMNH). *Campeche.* San José (AMNH); 6 km W of Francisco Escarcega, ♀ (MCZ). *Yucatan.* Chichen Itza (AMNH); Cardillera Mayapán (AMNH); Colonia Yucatan, ♂ (MCZ). *Quintana Roo.* Tumba (AMNH); Tancah (MCZ). *Chiapas.* Escuintla (MCZ); Ocosingo (AMNH); Huehuetán (AMNH); 105 km SE Palenque, ♀ (MCZ). GUATEMALA: Variedades (AMNH); Chicacao; Amatitlán (AMNH); Tikal, 2♀ (EMUC); Nueva Concepcion, ♀ (CAS). HONDURAS: Lancetilla (MCZ). Tela, (MCZ). COSTA RICA: *Prov. Cartago.* Turrialba, ♀ (AMNH). *Guanacaste.* Bagaces, Palo Verde, ♀ (MCZ). *Puntarenas.* 24 km S of Volcán, 12 July 1970, ♀ (S. Riechert, SR).

The *gracilis* Group

The *gracilis* group is characterized by the distinct genitalia. In females, the bulge of the epigynum is drawn out into a laterally flattened tip, with the flat area slightly indented (Figs. 743–745, 748–750). The male palpus has a weakly sclerotized median apophysis bearing a soft white fin-

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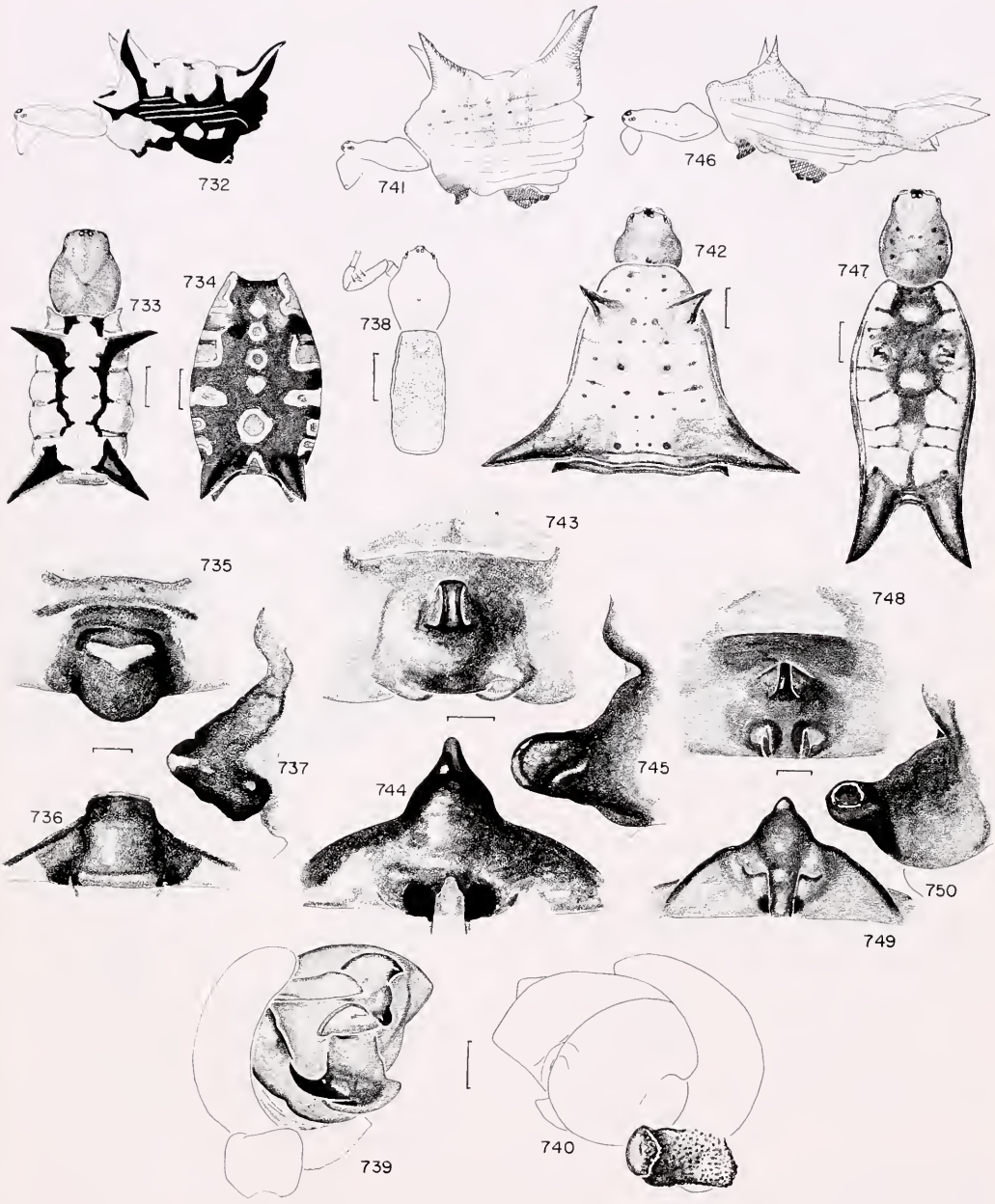
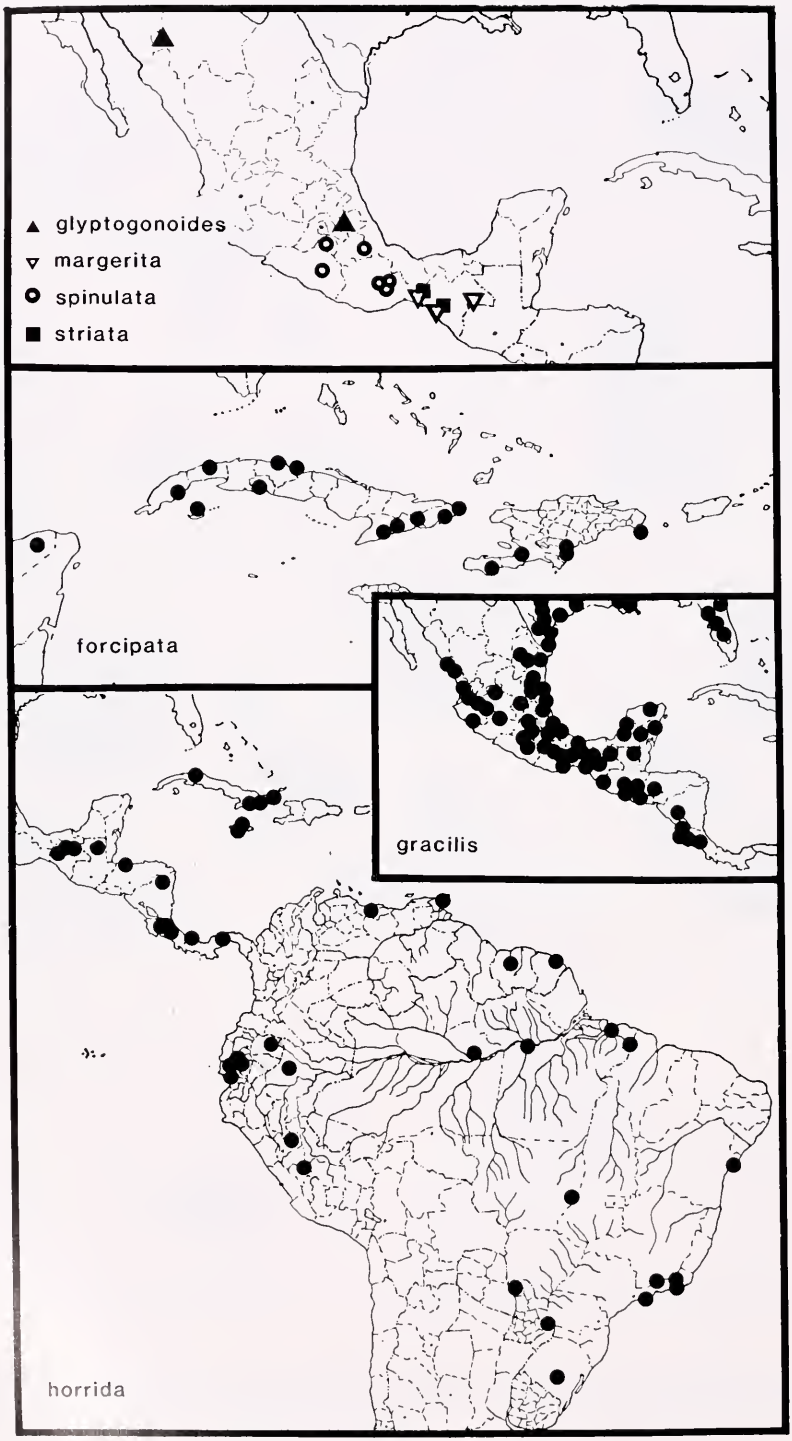
Figures 732–740. *Micrathena funebris* (Marx in Banks). 732–737. Female. 732. Lateral. 733. Dorsal (Chiapas). 734. Abdomen, dorsal (San Luis Potosí). 735. Epigynum, ventral. 736. Epigynum, posterior. 737. Epigynum, lateral. 738–740. Male. 738. Dorsal with first femur. 739. Left palpus, mesal. 740. Palpus, lateral.



Figures 741–745. *Micrathena striata* F. P.-Cambridge, female. 741. Lateral. 742. Dorsal. 743. Epigynum, ventral. 744. Epigynum, posterior. 745. Epigynum, lateral.

Figures 746–750. *Micrathena margerita* n. sp., female. 746. Lateral. 747. Dorsal. 748. Epigynum, ventral. 749. Epigynum, posterior. 750. Epigynum, lateral.

Scale lines. 0.1 mm, except Figures 732–734, 738, 741, 742, 746, 747, 1.0 mm.



Map 13. Distribution of *Micrathena* species of the *gracilis* group.

ger (Figs. 768, 772, 782). The palpal tibia is not modified (not drawn out distally on its mesal side). Most parts of the palpus appear weakly sclerotized.

The abdomen of all females has the ring around the spinnerets only lightly sclerotized. Males have a rectangular to elongate abdomen that may be posteriorly segmented (Figs. 767, 771, 781). All lack a hook on the first coxa and a corresponding groove on the second femur.

Diagnostic features for species are, in females, the number and shape of abdominal spines (Figs. 742, 752, 757, 763, 777). In males the easiest diagnostic feature is the shape of the paracymbium (Figs. 769, 773, 783), and perhaps the shape of the abdomen (Figs. 767, 771, 781).

Specimens collected together are generally similar. The extreme variation in shape of the female abdomen in several species (*M. forcipata*, Figs. 762, 763; *M. gracilis* and *M. horrida*, Figs. 774–777) is unusual.

Most species are found in southern Mexico and Guatemala. Only one, *M. horrida*, is found in South America (Map 13).

KEY TO THE *GRACILIS* GROUP

Females

1. Abdomen as long as wide, with only four humps (Figs. 756, 757); Mexico, Map 13 ..... *glyptogonoides*
– Abdomen usually longer than wide, with six or more humps or spines (Figs. 741, 746, 751, 770, 774) 2
2(1) Abdomen with six humps (rarely eight) or spines 3
– Abdomen with at least 10 humps or spines 6
3(2) Second pair of spines with granular texture, often with neck and widest near tip (Figs. 762, 763); Yucatan, Cuba, Hispaniola, Map 13 ..... *forcipata*
– Second pair of spines smooth and without neck; Mexico and Central America 4
4(3) Spines small and subequal in size (Figs. 751, 752); Central Mexico, Map 13 ..... *spinulata*
– First and second pair of spines much larger than third (Figs. 741, 746) 5
5(4) Abdomen length twice width, slightly constricted before posterodorsal spines (Fig. 747); Chiapas, Map 13 ..... *margerita*
– Abdomen length at most one and a half times width, without posterodorsal constriction (Fig. 742); Chiapas, Guatemala, Map 13 ..... *striata*
6(2) Abdomen with 12 or more humps or spines (Figs. 774–777), and with ventral hump behind spinnerets (Figs. 774, 775); Mexico, West Indies to southeastern Brazil, Map 13 ..... *horrida*
– Abdomen with 10 humps or spines, without ventral hump behind spinnerets (Fig. 770); eastern North America to Costa Rica, Map 13 ..... *gracilis*

Males

(Only the males of *M. forcipata*, *M. gracilis* and *M. horrida* are known.)

1. Posterior end of abdomen truncate (Fig. 767); paracymbium a flat lobe without keel (Fig. 769); Yucatan, Cuba, Hispaniola, Map 13 ..... *forcipata*
– Posterior end of abdomen appearing segmented (Figs. 771, 781); paracymbium with a keel (Figs. 773, 783) 2
2(1) Base of paracymbium with a keel parallel to axis of cymbium, next to a flat lobe (Fig. 783); conductor below embolus (in middle of palpus in mesal view) with single thorn (Fig. 782); Mexico, West Indies to southeastern Brazil, Map 13 ..... *horrida*
– Base of paracymbium with a keel at right angles to cymbium axis; paracymbium hook-shaped (Fig. 773); conductor below embolus with a parallel, sclerotized piece above thorn (Fig. 772); eastern North America south to Costa Rica, Map 13 ..... *gracilis*

Micrathena striata F. P.-Cambridge
Figures 741–745; Map 13

Micrathena striata F. P.-Cambridge, 1904: 530, pl. 50, fig. 6, ♀. Female syntype from Chichochoc [? locality not found], Guatemala (BMNH), examined. Roewer, 1942: 964. Bonnet, 1957: 2879. Chickering, 1961: 460, figs. 185–188, ♀.

Note. Chickering designated a lectotype; this was not seen. There are also three female specimens in the British Museum without locality labels.

Description. Female syntype. Carapace, legs orange-brown. Sternum blackish brown. Dorsum of abdomen with yellowish white pigment; spines orange; venter black. Carapace with a circular median thoracic depression; rim indistinct in dorsal view. Abdomen with two pairs of large dorsal spines, posterolaterals largest, and one pair of small posterior spines (Figs. 741, 742). Total length, 6.6 mm.

Carapace, 2.4 mm long, 1.9 mm wide. First femur, 2.4 mm; patella and tibia, 2.4 mm; metatarsus, 1.6 mm; tarsus, 0.8 mm. Second patella and tibia, 2.2 mm; third, 1.4 mm. Fourth femur, 2.7 mm; patella and tibia, 2.3 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm.

Variation. Females vary in total length from 6.6 to 9.2 mm. Posterodorsal spines face laterally on the syntype from Chichochoc (Fig. 742).

Diagnosis. Micrathena striata differs from *M. spinulata* by having the first two pairs of spines much larger than the third (Figs. 741, 742); it differs from *M. margerita* by lacking dimples on the carapace and by its shorter, more compact abdomen (Figs. 741, 742).

Natural History. A specimen was collected in cloud forest in Chiapas.

Distribution. Southern Mexico, Guatemala (Map 13).

Records. MEXICO: *Est. Chiapas.* 21 km W of Rizo de Oro, Oaxaca border, 1,615 m, 6 Sept. 1972, ♀ (C. Mullinex, K. Lucas, CAS); Finca Patichuiz, 53 km NE Las Margeritas, 2,000 m, 22 Oct. 1962, ♀ (A. Gardner, JAB).

Micrathena margerita new species
Figures 746–750; Map 13

Holotype. Female from Finca Patichuiz, 33 mi. [53 km] NE of Las Margeritas, 6,000 ft. [2,000 m], Chiapas, Mexico, 11 Oct. 1962 (A. Gardner, MCZ). The specific name is a noun in apposition after the type locality.

Description. Carapace orange, dusky black in thoracic region. Sternum black. Coxae orange. Legs dusky orange, first two femora darkest. Dorsum of abdomen with white patches on black; sides dark; venter black with three pairs of indistinct light patches. Carapace with three pairs of dimples and distinct thoracic depression; thorax high. Eyes subequal in size. Abdomen longer than wide, branched behind, with a pair of spines one third from anterior and one pair below branches. Total length, 8.0 mm. Carapace, 2.6 mm long, 1.9 mm wide. First femur, 2.5 mm; patella and tibia, 2.4 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm. Second patella and tibia, 2.2 mm; third, 1.4 mm. Fourth femur, 3.0 mm; patella and tibia, 2.3 mm; metatarsus, 1.8 mm; tarsus, 0.7 mm.

Diagnosis. This species differs from *M. striata* by its slender, biforked abdomen, and by having dimples on the carapace (Figs. 246, 247).

Natural History. One collection comes from a cloud forest.

Distribution. Chiapas, Mexico (Map 13).

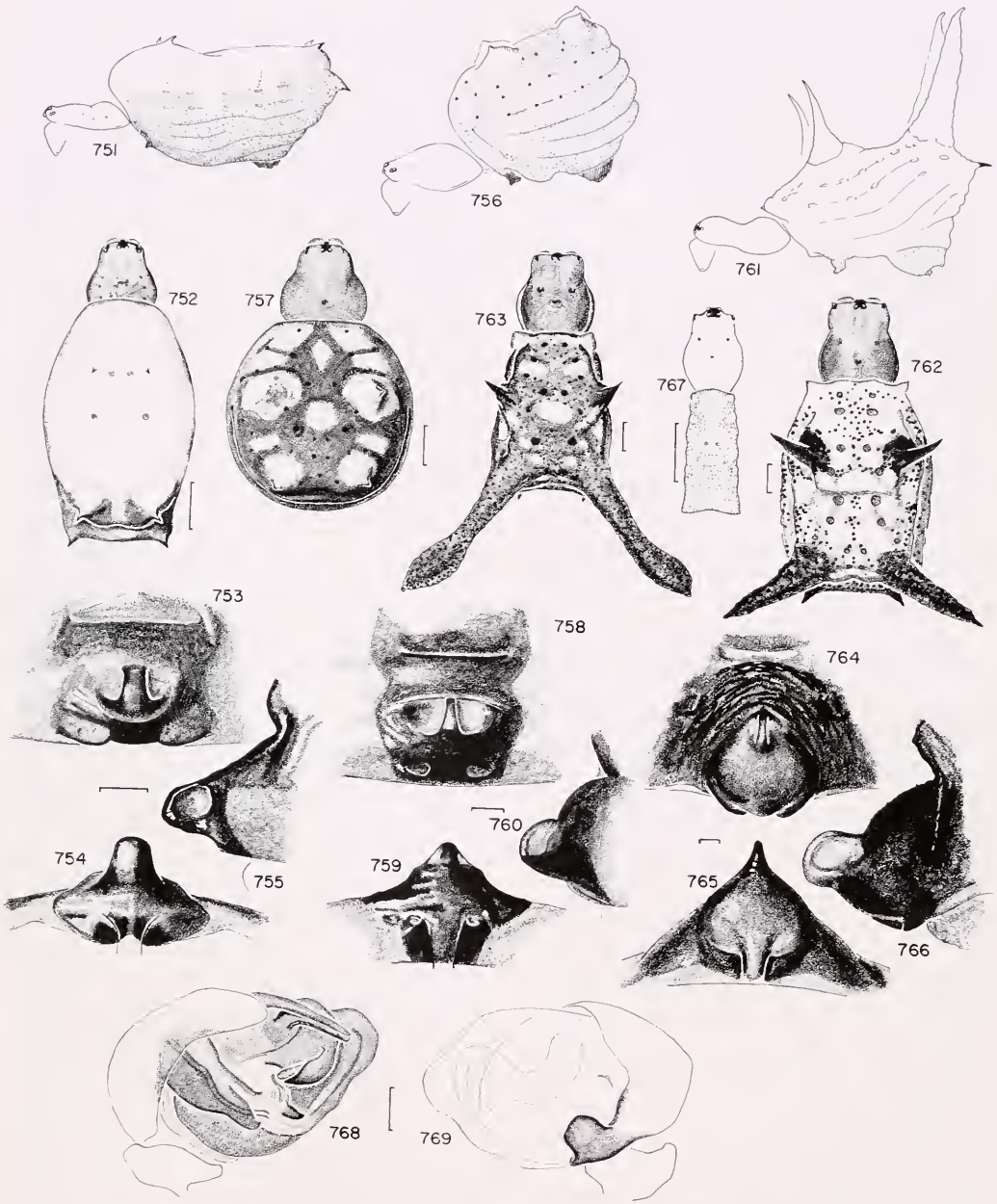
Paratypes. MEXICO: *Est. Chiapas.* 53 km NE of Las Margeritas, 2,000 m, 11 Oct. 1962, 3♀, 22 Oct. 1962, ♀ (A. Gardner, JAB); 21 km W Rizo de Oro, Oaxaca border, 1,615 m, 6 Sept. 1972, 2♀ (C. Mullinex, K. Lucas, CAS); Lago Tziscao, Montebello, 17–18 Aug. 1973, ♀ (P. Brignoli, PMB).

Micrathena spinulata F. P.-Cambridge
Figures 751–755; Map 13

Micrathena spinulata F. P.-Cambridge, 1904: 530, pl. 50, fig. 7, ♀. Four female syntypes from Amula [Guerrero, 17°38′: 9°15′], one syntype from Omilteme [Guerrero, WSW of Chilpancingo, 2,400 m el.], Mexico (BMNH), examined. Roewer, 1942: 964. Bonnet, 1957: 2879. Chickering, 1961: 459, figs. 181–184, ♀.

Description. Carapace, legs orange-brown. Sternum black. Dorsum of abdomen white, posteriorly black. Sides, venter black with three indistinct pairs of light patches on venter. Carapace with three pairs of dimples and distinct median thoracic depression; rim indistinct. Abdomen longer than wide, with three pairs of tiny spines, two pairs of which face posterior (Figs. 751, 752). Total length, 6.3 mm. Carapace, 1.9 mm long, 1.6 mm wide. First femur, 1.9 mm; patella and tibia, 1.8 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm. Second patella and tibia, 1.7 mm; third, 1.0 mm. Fourth femur, 2.3 mm; patella and tibia, 1.7 mm; metatarsus, 1.3 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 5.4 to 6.3 mm. Some specimens have



Figures 751–755. *Micrathena spinulata* F. P.-Cambridge, female. 751. Lateral. 752. Dorsal. 753. Epigynum, ventral. 754. Epigynum, posterior. 755. Epigynum, lateral.

Figures 756–760. *Micrathena glyptogonoides* n. sp., female. 756. Lateral. 757. Dorsal. 758. Epigynum, ventral. 759. Epigynum, posterior. 760. Epigynum, lateral.

Figures 761–769. *Micrathena forcipata* (Thorell). 761–766. Female. 761. Lateral. 762, 763. Dorsal. 764. Epigynum, ventral. 765. Epigynum, posterior. 766. Epigynum, lateral. 767–769. Male. 767. Dorsal. 768. Left palpus, mesal. 769. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 751, 752, 756, 757, 761–763, 767, 1.0 mm.

paired black patches on the dorsum. The illustrations were made from the Amula syntype.

Diagnosis. *Micrathena spinulata* differs from *M. striata* and *M. margerita* by having all six spines the same size (Figs. 751, 752).

Distribution. South-central Mexico (Map 13).

Records. MEXICO: *Est. Veracruz.* pass above Orizaba, 1,900 m, 29 June 1944, ♀ (L. I. Davies, AMNH). *Morelos.* Tepoztlan, 1,600 m, 2 Aug. 1942, 3♀ (C. Bolivar, M. Santullano, AMNH). *Guerrero.* 18 km W of Chilpancingo, 30 July 1956, ♀ (W. Gertsch, V. Roth, AMNH).

Micrathena glyptogonoides new species
Figures 756–760; Map 13

Holotype. Female from Necaxa, Pueblo, Mexico, 23 September 1972 (collector unknown, AMNH). The specific name was a manuscript name applied by A. F. Archer to this species.

Description. Female. Carapace, chelicerae, sternum, coxae and trochanters orange. Legs black. Dorsum of abdomen with paired and median white patches; sides and venter black without marks. Carapace high, median thoracic depression indistinct, no rim. Eyes subequal in size. Abdomen subspherical with two pairs of dorsal humps, each tipped by a tubercle (Figs. 756, 757). Total length, 6.7 mm. Carapace, 2.4 mm long, 2.2 mm wide. First femur, 1.9 mm; patella and tibia, 2.0 mm; metatarsus, 1.2 mm; tarsus, 0.7 mm. Second patella and tibia, 1.9 mm; third, 1.2 mm. Fourth femur, 2.2 mm; patella and tibia, 1.9 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm.

Variation. Paratypes have the sides and dorsum of abdomen light.

Diagnosis. This species differs from others of the *gracilis* group by the subspherical abdomen having only four humps (Figs. 756, 757). All other species have six or more spines or humps.

Paratypes. MEXICO: *Est. Chihuahua.* La Polvosa, 1,950 m, 108°39′W, 28°9′N, 16 Aug. 1958, 3♀ (L. R. Commisoris, AMNH).

Micrathena forcipata (Thorell)
Figures 761–769; Map 13

Acrosoma forcipatum Thorell, 1859: 300. Female type from Cuba, lost.

Acrosoma flavomaculatum Keyserling, 1864: 77, pl. 2, fig. 10, ♀. Female holotype from Haiti (BMNH), examined. Keyserling, 1892, 4: 24, pl. 1, fig. 21, ♀.

Micrathena cylindracea Franganillo, 1930: 76; 1936: 96. Juvenile (?) from Sierra Maestra, Cuba, lost. First synonymized by Bryant.

Micrathena forcipata:—Bryant, 1940: 372, figs. 149, 151 (not figs. 141, 146, male). Chickering 1964: 257, figs. 11–15, ♀ (not male).

Micrathena bryantae Chickering, 1964: 254, figs. 1–3, ♂. Male holotype from Los Llanos [Prov. Guantánamo], Cuba, 1,000–2,000 ft. [300–600 m] (MCZ), examined. NEW SYNONYMY.

Synonymy. Chickering's *M. bryantae* is the male of this species.

Description. Female. Carapace, sternum, legs brown. Dorsum of abdomen white with brown to black patches; spines orange; venter black with paired white spots. Carapace with thoracic depression, one pair of dimples; thorax high with narrow rim. Abdomen with two pairs of dorsal spines and one small pair posteriorly, sometimes with small anterior spines overhanging carapace (Figs. 761–763). Total length, 8.5 mm. Carapace, 3.1 mm long, 2.6 mm wide. First femur, 2.8 mm; patella and tibia, 2.8 mm; metatarsus, 2.0 mm; tarsus, 0.7 mm. Second patella and tibia, 2.6 mm; third, 1.5 mm. Fourth femur, 3.9 mm; patella and tibia, 3.0 mm; metatarsus, 2.4 mm; tarsus, 0.9 mm.

Male. Carapace rich dark brown, sternum blackish brown. Legs light brown. Dorsum of abdomen with a black pattern and white patches; venter gray. Carapace with circular thoracic depression and a pair of dimples. Sternum slightly rugose. Abdomen rectangular, sides slightly lobed (Fig. 767). Total length, 3.7 mm. Carapace, 1.5 mm long, 0.9 mm wide. First femur, 1.2 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm. Second patella and tibia, 1.3 mm; third, 0.7 mm. Fourth femur, 1.6 mm; patella and tibia, 1.5 mm; metatarsus, 0.8 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 7.2 to 10.3 mm, males from 3.4 to 4.5 mm. The females may have small anterior spines, or these may be absent. Large posterodorsal spines are of variable length, sometimes much longer than the body, and often swollen at their tip (Figs. 762, 763).

Note. Males and females have been collected together.

Diagnosis. This species has genitalia similar to *M. gracilis* and *M. horrida*. Females differ by having the large posterolateral spines soft with tiny platelets, rugose in appearance (Figs. 762, 763). The male differs by the shape of the abdomen (Fig. 767), by the mitten-shaped paracymbium (Fig. 769) and by the shape of the conductor (Fig. 768).

Distribution. Yucatan, Cuba and Hispaniola (Map 13).

Records. MEXICO: *Est. Yucatan.* Coscomatepec [?], 25 Aug. 1963, ♀ (D. L., H. E. Frizzell, EPC). CUBA: *Prov. Santiago de Cuba.* Cuchillo de Guájimero, 600 m, 22 July 1936, ♀ (P. J. Darlington, MCZ); Sierra Maestra, 15–20 May 1948, ♀ (G. Acuna, MCZ); coast below Pico de Turquino, 1936, ♀ (P. J. Darlington, MCZ). *Guantánamo.* Los Llamos, 300–600 m, 16–20 July 1936, 3♀ (P. J. Darlington, MCZ); mts. north of Imías, 25–28 July 1936, 2♀ (P. J. Darlington, MCZ). *Habana.* Havana, ♀ (Baker, MCZ). *Ciego de Avila.* Cayo La Salina, ♀ (MCZ). *Cienfuegos.* Soledad (sev. coll., MCZ, CASH). *Pinar del Río.* Galalon, juv. (P. Berm, MCZ); Sierra del Rosario, Inst. Botany, ♀ (R. Levins, MCZ); Cuajani, 13 Jan. 1974, 2♀ (G. Alayón, CASH). *Isla de Pinos.* 1918, 2♀ (T. Barbour, MCZ); Sierra Isabelita, La Fe, 27 April 1974, ♀ (M. Diaz, CASH); Sierra Caballos, 16 June 1974, 3♀, ♂ (F. Armas, CASH). *Villa Clara.* Vega Alta, ♀ (P. Bermudez, AMNH). *Granma.* Uvero, Las Virgenes, Sierra Maestra, 700 m, 25 May 1972, ♀ (G. Alayón, CASH). HAITI: 3 km E of Cayes du Jacmel, 2 Sept. 1935, ♀ (W. G. Hassler, AMNH). Carrefour, 22 July 1955, ♀ (A. F. Archer, AMNH). DOMINICAN REPUBLIC: *Barahona.* Mt. Busú, Sierra Martín García, June 1983, ♀ (G. Flores, MCZ); 3 km S of Barahona, 16 Aug. 1935, ♀ (W. Hassler, AMNH). *La Altagracia.* Isla Saona, 18 July 1974, ♀ (J. A. Steinwalder, MNSD).

Micrathena gracilis (Walckenaer)
Figures 770–773; Map 13

Epeira gracilis Walckenaer, 1805: 65. Female from Carolina, lost.

Acrosoma matronale C. L. Koch, 1845: 68, fig. 887, ♀. Female from Mexico (ZMB), examined.

Micrathena nigrior Chamberlin and Ivie, 1936: 58, figs. 134, 135, ♀. Four female syntypes from Barro Colorado Island, Gatún Lake, Panama (AMNH), examined.

Micrathena gracilis:—Levi, 1978: 433, figs. 55–68, ♀, ♂, map 2.

Synonymy. Despite the large collections available, no other specimens of this species were found from Barro Colorado Island. The locality of *M. nigrior* may be in error.

Diagnosis. Females differ from *M. horrida* by having only ten spines or humps on the abdomen, and by lacking a hump behind the spinnerets (Fig. 770). Immature females also lack this hump, present in *M. horrida*. Males differ by the shape of the paracymbium (Fig. 773) and of the conductor below the embolus (Fig. 772). Also, in mesal view the embolus appears filamentous (Fig. 772).

Distribution. Eastern North America south to Costa Rica (Levi, 1978) (Map 13).

Records. MEXICO: *Est. Tamaulipas.* Tampico; 100 km S Ciudad Victoria; N of Antiguo Morelos; 26 km WNW Ocampo. *Nuevo León.* Linares; 30 km S of Monterrey; San Nicolás de los Garza. *San Luis Potosí.* 5 km W El Naranjo; Valles. *Sinaloa.* Elota; Mazatlan; 20 km N Elota. *Guanajuato.* Silao. *Nayarit.* Tepic; Compostela; Jalisco. *Jalisco.* Guadalajara; Lagos de Moreno; S side Lago Chapala; San Juan de los Lagos; La Floresta. *Veracruz.* common. *Distrito Federal.* Ciudad Mexico. *Michoácan.* Pátzcuaro; Uruapan. *Puebla.* Acatlan. *Morelos.* Cuernavaca. *Guerrero.* Teloloapán; Taxco; Chilpancingo. *Oaxaca.* common. *Campeche.* Lerma;

San José; Campeche; Chicanna ruins, 8 km W Xpujil. *Yucatan.* Chichen Itza; Pisté; 3 km E of Chichen Itza. *Quintana Roo.* Esmerelda; Tumba; Kohunlich ruins, 9 km S Francisco villa. *Chiapas.* common. GUATEMALA: *Dept. El Petén.* Tikal. *Guatemala.* Guatemala City. *Santa Rosa.* Variedades. *Chiquimula.* Chiquimula. BELIZE: Belize. HONDURAS: Zambrano. EL SALVADOR: San Salvador; Quezaltepeque; La Libertad. NICARAGUA: Masatepe. COSTA RICA: *Prov. Alajuela.* Atenas. *Guanacaste.* Cañas; Prov. Santa Rosa N.P.; Bedero; Playa Hermosa, 20 m; Liberia. *San José.* San José; San Antonio de Escazú, 1,350 m.

Micrathena horrida (Taczanowski) Figures 774–783; Map 13

Acrosoma horrida Taczanowski, 1873: 281, pl. 6, fig. 31, ♀. Female holotype from Cayenne, French Guiana (PAN), examined.

Acrosoma raceminum Butler, 1873: 427. Female holotype (in poor condition, with pinhole in abdomen) from Orinoco, Venezuela (BMNH), examined. NEW SYNONYMY.

Acrosoma mammillata Butler, 1873: 427. Female holotype (abdomen only) from Santarém, Brazil (BMNH), examined.

Acrosoma longicaudum O. P.-Cambridge, 1890: 61, pl. 8, fig. 9, ♂. Male holotype from Bugaba, Panama (BMNH), lost. Keyserling, 1892: 15, pl. 1, fig. 11, ♂. F. P.-Cambridge, 1904: 530, pl. 50, fig. 5, ♂.

Micrathena horrida:—Simon, 1895: 851, figs. 898, 919, ♀. Petrunkevitch, 1910: 212, pl. 21, figs. 9–11, ♀. Reimoser, 1917: 959. Bonnet, 1957: 2870. Chickering, 1961: 424, figs. 83–88, ♀, ♂.

Micrathena simoni Petrunkevitch, 1910: 213. New name for Simon's (1895) illustration figs. 898, 919 of *M. horrida.*

Micrathena gracilis:—Franganillo, 1936: 98 (misidentification)

Micrathena mammillata:—Bryant, 1940: 374, figs. 142, 147, 155, ♀, ♂.

Micrathena multituberculata di Caporiacco, 1947: 25. Female holotype from British Guyana (MZUF), examined. 1948: 665, figs. 75–78, ♀. NEW SYNONYMY.

Note. The type of *A. longicaudum* is lost, but a specimen of O. P.-Cambridge with the name comes from Teapa, Mexico. The specimens of *A. raceminum* and *M. multituberculata* are within the variation and range of *M. horrida.*

Description. Female from Panama. Carapace orange-brown, sclerotized areas darker brown, with some dark gray markings above rim of carapace; rim light. Sternum, legs orange-brown. Abdomen gray to orange with some black marks. Total length, 7.5 mm. Carapace, 3.3 mm long, 2.3 mm wide. First femur, 2.1 mm; patella and tibia, 2.2 mm; metatarsus, 1.3 mm; tarsus, 0.7 mm. Second patella and tibia, 1.9 mm; third, 1.3 mm. Fourth femur, 2.7 mm; patella and tibia, 2.2 mm; metatarsus, 1.4 mm; tarsus, 0.8 mm.

Male from Panama. Carapace brown. Sternum grayish brown. Legs lighter brown. Abdomen brown with white patches along margin, some gray and black pigment above. Carapace and abdomen corniculate. Thorax with a distinct depression and a pair of dimples. Abdomen long, segmented posteriorly (Fig. 781). Total length, 4.5 mm. Carapace, 1.2 mm long, 0.7 mm wide. First femur, 0.7 mm; patella and tibia, 0.8 mm; metatarsus, 0.4 mm; tarsus, 0.3 mm. Second patella and tibia, 0.6 mm; third, 0.4 mm. Fourth femur, 0.9 mm; patella and tibia, 0.6 mm; metatarsus, 0.6 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 7.0 to 11.5 mm, males from 4.5 to

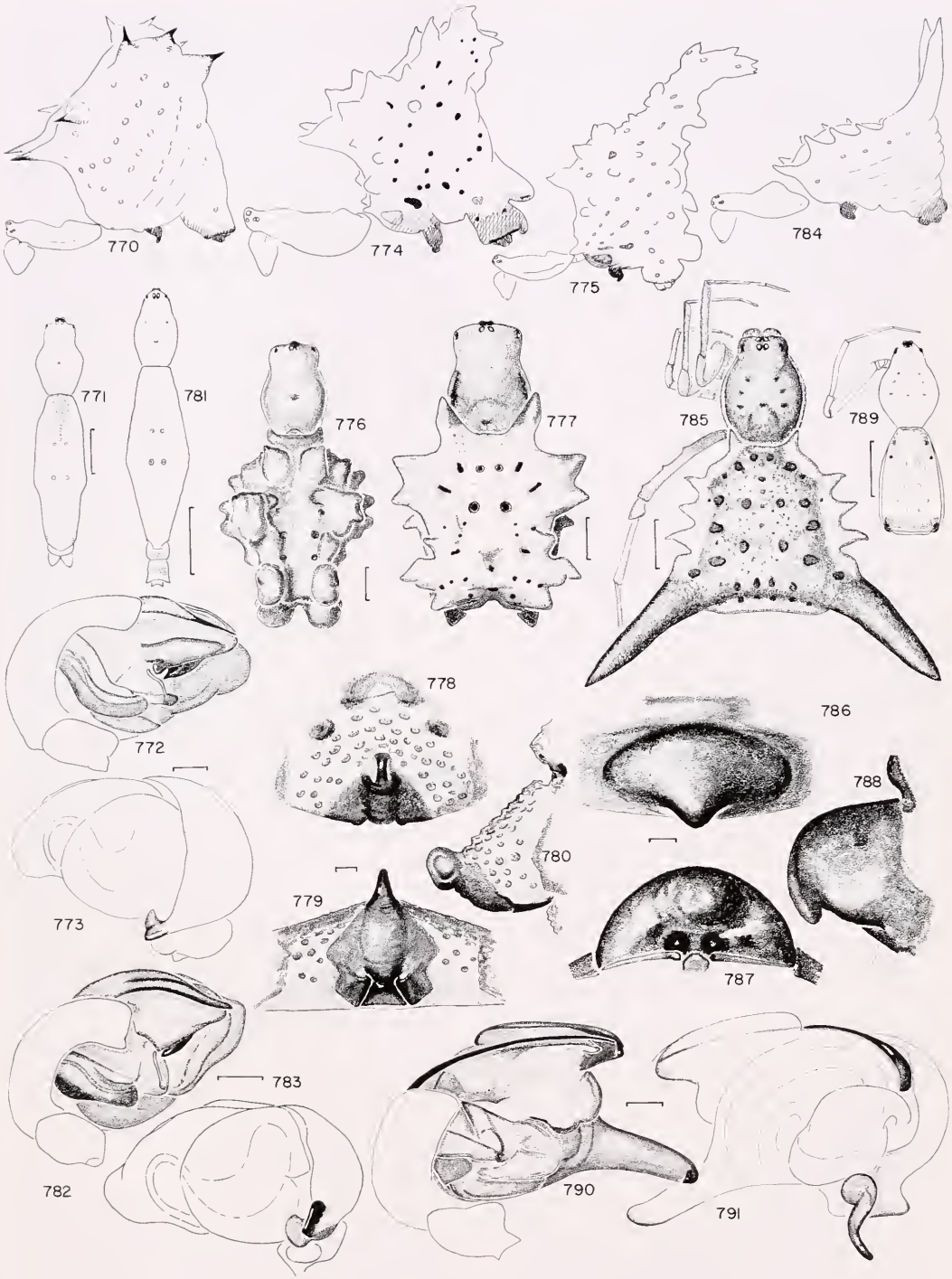
→

Figures 770–773. *Micrathena gracilis* (Walckenaer). 770. Female, lateral. 771–773. Male. 771. Dorsal. 772. Left palpus, mesal. 773. Palpus, lateral.

Figures 774–783. *Micrathena horrida* (Taczanowski). 774–780. Female. 774, 775. Lateral. 776, 777. Dorsal. 774, 777. (Panama). 775, 776. (Orinoco, Venezuela). 778. Epigynum, ventral. 779. Epigynum, posterior. 780. Epigynum, lateral. 781–783. Male. 781. Dorsal. 782. Palpus, mesal. 783. Palpus, lateral.

Figures 784–791. *Micrathena pungens* (Walckenaer). 784–788. Female. 784. Lateral. 785. Dorsal. 786. Epigynum, ventral. 787. Epigynum, posterior. 788. Epigynum, lateral. 789–791. Male. 789. Dorsal. 790. Palpus, mesal. 791. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 770, 771, 774–777, 781, 784, 785, 789, 1.0 mm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5.0 mm. Some individuals have a bold pattern of black patches on white on the dorsum of the abdomen. The carapace at times has dimples. The abdomen of females has slender humps (Fig. 777), swollen humps (Fig. 776), or at times has a tail (Fig. 775).

Note. There are numerous collections of this common species having both male and female individuals.

Diagnosis. This species can be confused with *M. gracilis*. *M. horrida* has twelve or more humps on the abdomen, often many more (Figs. 774–777), whereas *M. gracilis* has only ten. Also, *horrida* females always have a hump behind the spinnerets (Figs. 774, 775), while *gracilis* does not. The hump is present in immatures.

The male can be separated by the paracymbium having a keel almost parallel to the axis of the cymbium, and a flat lobe next to it (Fig. 783); *M. gracilis* has a hook-shaped paracymbium with a keel almost at right angles to the axis of the cymbium. The embolus of *M. horrida* is a wide and semi-transparent structure (Fig. 782); the conductor behind and below the embolus has a sclerotized tooth of variable shape (in the middle of the palpus in Fig. 782). The embolus of *M. gracilis*, on the other hand, is a black filament, the conductor having a double lobed, sclerotized structure.

Natural History. Micrathena horrida is found in forests.

Distribution. Cuba, Jamaica, Chiapas, Mexico to Paraguay (Map 13).

Records. MEXICO: *Chiapas.* Palenque ruins, May 1980, imm. (J. Coddington, MCZ); Pichucalco, 17 July 1947, ♀ (C. M. Goodnight, AMNH); 32 km NW Ocozocoautla, 27 Aug. 1972, ♀ (CAS). GUATEMALA: *Dept. El Petén.* Uaxactún (MCZ). HONDURAS: Lacetilla (MCZ). NICARAGUA: Musawas, Waspuc River (AMNH). COSTA RICA: *Prov. Heredia.* Puerto Viejo, La Selva (MZCR). *Limón.* 20 km N Siquirres, 100 m, July 1980 (MCZ); Hamburg Farm (NMW). *Cartago.* Turrialba. *San José.* San Isidro del General (MCZ). *Puntarenas.* Esparta (MCZ). PANAMA: *Cocle Prov.* El Valle, ♀ (AMNH). *Panamá.* many collections. CUBA: *Prov. Santiago de Cuba.* Pico Turquino (MCZ); Gran Piedra, 1,200 m (MCZ, CASH); Cuchillo de Guajimero, 600 m (MCZ); Puerto Boniato (MCZ). *Habana.* Tapaste (CUC). *Guantánamo.* Los Llanos (MCZ). JAMAICA: *St. Ann Parish.* Diablo Forest Reserve (AMNH). *St. Catherine.* Rio Cobre Gorge nr. Spanish Town (IJK). LESSER ANTILLES: *Trinidad.* Simla (AMNH); Arima Valley (AMNH). VENEZUELA: Maracay (MCZ); Caracas (NMW). SURINAME: *Saramacca Prov.* Voltzberg-Raleighvallen Res. (MCZ). COLOMBIA: Bugabita [?] (NMW). ECUADOR: *Est. Los Ríos.* Juan Montalvo (AMNH). *Napo.* Tarapuy (MECN). *Guayas.* Milagro (EPC). *Puna Island.* (EPC). *Bolívar.* Balzapamba, 700–800 m (AMNH). PERU: *Dept. Loreto.* Pastaza (MCZ). *Junín.* 29 km NE La Merced (CAS). *Huánuco.* Monsón Valley, Tingo María (CAS). BRAZIL: *Est. Pará.* 12 km W of Canindé (AMNH); Belém (MEG, AMNH); Santarém (BMNH); Rio Gurupi (MZSP). *Amazonas.* Manaus (NRS). *Bahia.* Urolinea Salvador (MACN). *Mato Grosso.* Chavantina (MZSP). *Rio de Janeiro.* Barra da Tijuca (MCZ); Rio de Janeiro (MNRJ); Pinheiro (MNRJ); Niterói (MNRJ); Petrópolis (MNRJ); Angra dos Reis (Praia do Leste) (MZSP). *São Paulo.* Ilha São Sebastião (MZSP). *Rio Grande do Sul.* Rambo (MNRJ). PARAGUAY: (BMNH) *Dept. Concepción.* Territ. Fonciére (NMW, MCZ). ARGENTINA: *Prov. Misiones.* Río Iguazú, 60 km from Pto. Iguazú, 5 March 1957 (E. W. Partridge, MACN).

Micrathena pungens (Walckenaer)
Figures 784–791; Map 14

Plectana pungens Walckenaer, 1841: 173. Female specimen from Cayenne, French Guyana, lost.

Acrosoma pungens:—Keyserling, 1863: 72, pl. 2, fig. 5, ♀; 1892: 29, pl. 1, fig. 26, ♀.

Acrosoma luctuosa Taczanowski, 1873: 267, pl. 5, fig. 21, ♀. Eleven female syntypes from Cayenne

and St. Laurent de Maroni, French Guiana (PAN), examined. First synonymized by Chickering, 1960c.

Micrathena luctuosa:—Reimoser, 1917: 134. Roewer, 1942: 960. Bonnet, 1957: 2871.

Micrathena pungens:—Reimoser, 1917: 134. Roewer, 1942: 962. Bonnet, 1957: 2874. Chickering, 1960c: 85, figs. 76–79, ♀.

? *Micrathena carvalhoi* Mello-Leitão, 1944a: 9. Female holotype from Barra do Tapirapés [Est. Mato Grosso], Brazil (MNRJ), lost. NEW SYNONYMY.

Description. Female syntype of *M. luctuosa*. Carapace, sternum, legs brown. Dorsum of abdomen brownish black with a white band along lateral margin, including four pairs of lateral spines, and a transverse white band on posterior margin (Fig. 785); venter and sides black; sclerotized areas brown. Carapace with three pairs of dimples, the first most distinct, a circular thoracic mark and a light colored rim. Abdomen with an anterior pair of spines overhanging carapace, three pairs of spines on sides, and one large posterolateral black spine whose base has a little hump anteriorly (Fig. 785). Total length, 5.8 mm. Carapace, 2.3 mm long, 1.8 mm wide. First femur, 2.0 mm; patella and tibia, 2.3 mm; metatarsus, 1.4 mm; tarsus, 0.6 mm. Second patella and tibia, 1.9 mm; third, 1.2 mm. Fourth femur, 2.5 mm; patella and tibia, 2.1 mm; metatarsus, 1.4 mm; tarsus, 0.6 mm.

Male from Suriname. Carapace yellowish. Sternum white, dusky all around. Legs yellowish, femora dusky. Dorsum of abdomen with some white pigment spots anterolaterally; dusky anterior and posterior (Fig. 789); venter black except square orange area between epigastric groove and spinnerets. Carapace with three pairs of dimples and circular thoracic depression. Without coxal hook. Abdomen longer than wide, widest behind, and smooth, without spines (Fig. 789). Total length, 3.4 mm. Carapace, 1.6 mm long, 1.0 mm wide. First femur, 1.4 mm; patella and tibia, 1.5 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm. Second patella and tibia, 1.2 mm; third, 0.7 mm. Fourth femur, 1.3 mm; patella and tibia, 1.1 mm; metatarsus, 0.7 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 5.5 to 7.0 mm, males 3.4 to 3.5 mm. Some older adult females have two large transverse dorsal sclerites anteriorly on the abdomen. Immature specimens have the large posterolateral spine much shorter, and have two pairs of spines on the posterior slope of the abdomen. These at times remain as small teeth or sclerotized humps in the adult. In many specimens, especially those from the Pará state, Brazil, the tip of the large spine is offset anteriorly.

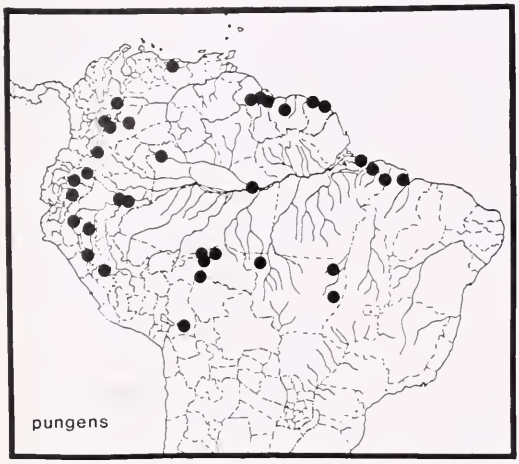
Note. According to a note in a vial, Harriet Exline found a palp in the epigynum in a female from Divisoria, Huánuco, Peru. A male was collected with females in Suriname, another in Mato Grosso. The males were first thought to be those of *Chaetacis abrahami*; its association with *M. pungens* is uncertain.

Diagnosis. The female is readily separated from other species by having four pairs of light colored spines and a light colored hump on the sides of otherwise dark abdomen (Fig. 785), and by the epigynum whose tip is drawn out posteriorly, overhanging the openings on the posterior face (Figs. 786–788). The male has a palp like that of *Chaetacis* species, with a drawn out tegulum (Figs. 790, 791). It differs from males in *Chaetacis* by lacking spines or humps on the carapace.

Natural History. Specimens have been collected in forest savanna in Guyana and forest in Mato Grosso. One female was accompanied in the vial by a wrapped ant almost twice the length of the spider.

Distribution. From eastern Colombia, Venezuela, northeastern Brazil to Bolivia (Map 14).

Records. VENEZUELA: *Est. Aragua.* Rancho Grande, ♀, ♂ (MACN). GUYANA: Kuruabaru Riv., ♀ (BMNH); Kartabo (CUC); Rockstone (AMNH); Minnehaha Creek (AMNH); Kaietur (AMNH); Ikuruwa River (AMNH); Essequibo Riv. (AMNH). SURINAME: *Saramacca.* Voltzberg-Raleighvallen Reserve, ♀, Feb. 1982, ♀, ♂ (D. Smith, MCZ). COLOMBIA: *Dept. Meta.* Carimagua, ♀ (MCZ); Villa-



Map 14. Distribution of *Micrathena pungens*.

vicencio, ♀ (AMNH); 45 km W of Villavicencio (AMNH). *Boyacá-Santander.* Río Suárez, 800–1,000 m (AMNH). *Cundinamarca.* Bogotá, ♀ (NMW). *Caquetá.* Río Orteguaza, 200 m (AMNH). ECUADOR: *Prov. Napo.* Tarapuy, ♀ (MECN); Napo headwaters, Río Arajuno, 1,000 m (AMNH). *Morona-Santiago.* Wakani, Chiguaza, ♀ (MCZ). PERU: *Dept. Loreto.* Iquitos (MCZ); Río Bombo, Alto Tapiche (AMNH). *Amazonas.* Montenegro, Bagua (AMNH). *San Martín.* 30 km SE of Moyobamba, 20 km NE of Moyobamba (AMNH); Río Alto Marañón, Río Campo Nueva (AMNH). *Huánuco.* Divisoria (?) (AMNH). *Pasco.* Puerto Bermudez, Río Pichis (CUC). BRAZIL: *Est. Pará.* Belém (MCZ); 50 km E of Canindé, ♀ (AMNH); Cachoeira, 5♀ (IBSP); Rio Gurupi, 2♀ (MZSP). *Amazonas.* Taracuá, ♀ (NRS); Rio Negro, São Gabriel, 2♀ (NRS); Manaus, ♀, ♂ (MEG); Reserve Ducke, NNE of Manaus, ♂ (AMNH). *Rondônia.* Pôrto Velho, ♀ (MCZ); Abunã, ♀ (MCZ); Vila Murtinho, ♀ (MCZ). *Maranhão.* Chapade dos Guimarães, ♀ (AMNH). *Mato Grosso.* Aripuanã, ♀ (MCZ); 260 km N of Xavantina, Feb.–April 1969, juv. ♀, ♂ (Xavantino-Cachimbo Exped., MCZ). BOLIVIA: *Dept. Beni.* Vasa Diez, Cachuela Esperanza. April 1922, ♀ (J. H. Williamson, MCZ). *La Paz.* Coroico, ♀ (E. Reimoser, MCZ).

Chaetacis Simon

Chaetacis Simon, 1895: 863. Type species *Acrosoma affinis* C. L. Koch (=*C. aureola*) by original designation.

Diagnosis. Chaetacis species differ from other American Araneidae except *Micrathena* and *Gasteracantha* by having a sclerotized ring around the spinnerets. It differs from *Micrathena* and *Gasteracantha* by having swellings with tubercles or a prominent spine on each side of the head, behind the eyes (Figs. 792, 793, 803, 804, Table 3).

Description. Females of all species are 4.0 to 6.0 mm in total length, males between 2.5 and 4.0 mm.

All species have the carapace orange to orange-brown, the posterior of the thorax darker, and the rim and head swellings or spines lighter. The sternum in all species (except *C. woytkowskii*) is darker than the coxae, brown to black; the proximal articles of the legs are orange, distally darker brown to black. Appendages are never banded or striped. The abdomen is dorsally white with paired black patches, and the largest spines black. The sides and venter are dark with paired white patches. Sclerotized spots and disks are orange, the book-lung covers and ring around spinnerets often black.

In all females the carapace is longer than wide, with a prominent rim and a distinct round thoracic mark; the three pairs of dimples form grooves separated from each other by swellings. The head portion is smooth except for the pair of tubercular swellings or spines. The thorax may have additional indistinct tubercular swellings (*C. aureola*) or may be covered by small spines (Figs. 792, 793, 827, 828). The posterior median eyes are sometimes slightly larger than the anterior medians, both laterals or the posterior laterals only slightly smaller. The median eyes are their diameter of each pair apart. The fourth fe-

mur is slightly longer than the first. The proximal articles, including the coxae, are tuberculate, the fourth coxa and fourth femur most tuberculate or may have denticles.

The abdomen is covered by sclerotized disks characteristic also for *Micrathena*, as well as by rows of small disks on the sides, and tiny sclerotized spots in the dark colored areas of the dorsum, sides and venter. Unlike other Araneidae except *Micrathena*, the book-lung covers appear smooth and are covered by stridulating ridges only visible with a compound microscope (Plate 3). Tubercles on the fourth coxa or occasionally on the femur are presumably the pegs.

Males may have the carapace like that of the female, the swellings and tubercles less pronounced. There are distinct widely spaced teeth around the rim of most species (Figs. 818, 833). The legs are like those of the females but longer. The first coxa has no hook, the second femur no groove. Both endite and palpal femur lack the matching teeth. The first tibia is slightly sinuous in some males, strongly curved in *C. aureola* and *C. picta* (Figs. 833, 850). The abdomen of some species is smooth (Figs. 833, 850); others have pairs of spines like females (Figs. 809, 818).

Genitalia. The epigynum has a cone-shaped median bulge; on the posterior slope is a characteristic median plate. The bulge is truncate posteriorly (Figs. 806, 808) or pointed (Figs. 830, 832, 847–849). In the lateral borders of the posterior plate are the entrances to the short connecting canals. The seminal receptacles have distinctive shape and may be of diagnostic value (Figs. 794, 814). The profile of the epigynum is diagnostic (Figs. 797, 808, 817, 843).

The male palpus has a sclerotized embolus (Figs. 810, 819, 834) whose tip is held by a conductor. The tegulum has a tubular curved projection ventrally. There is an indistinct median apophysis having only a small sclerotized area. The paracymbium (Figs. 811, 820, 835, 836, 852, 861) is of distinctive shape in different species.

Species Differences. Species differ by the number of abdominal spines (Figs. 838, 845), and whether they have tubercles behind the eyes (Fig. 812) or a spine (Fig. 821). One female from "La Moka" [Caracas, Venezuela] (ZMK) had 13 spines on the abdomen: six left and seven right. The epigynum identified it as belonging to the 12-spined *C. carimagua*; some *C. aureola* also have 13 spines. Also, the tubercles and shape of the head spines are variable. Because the shape of the epigynum is also quite variable, the internal genitalia were illustrated; I am not certain if this is of value. Generally, specimens from one locality differ little from each other.

The males appear more distinct. Two species (*picta* and *aureola*) lack spines on the abdomen (Figs. 833, 850); *Chaetacis cucharas*, *C. cornuta* and *C. necopinata* have spines (Figs. 809, 818, 859). The paracymbium of palpi is also distinctively shaped (Figs. 811, 820, 835, 836, 852). Two species have the first tibia curved (*picta* and *aureola*). It may be that if more males were available, their placement would prove to be as uncertain as that of females.

Natural History. The long fourth femora suggest that *Chaetacis* hang in the web upside down with the abdomen held horizontal, as do *Micrathena*. However, little is known of the habits of the species.

Distribution. The genus is only known from the neotropics.

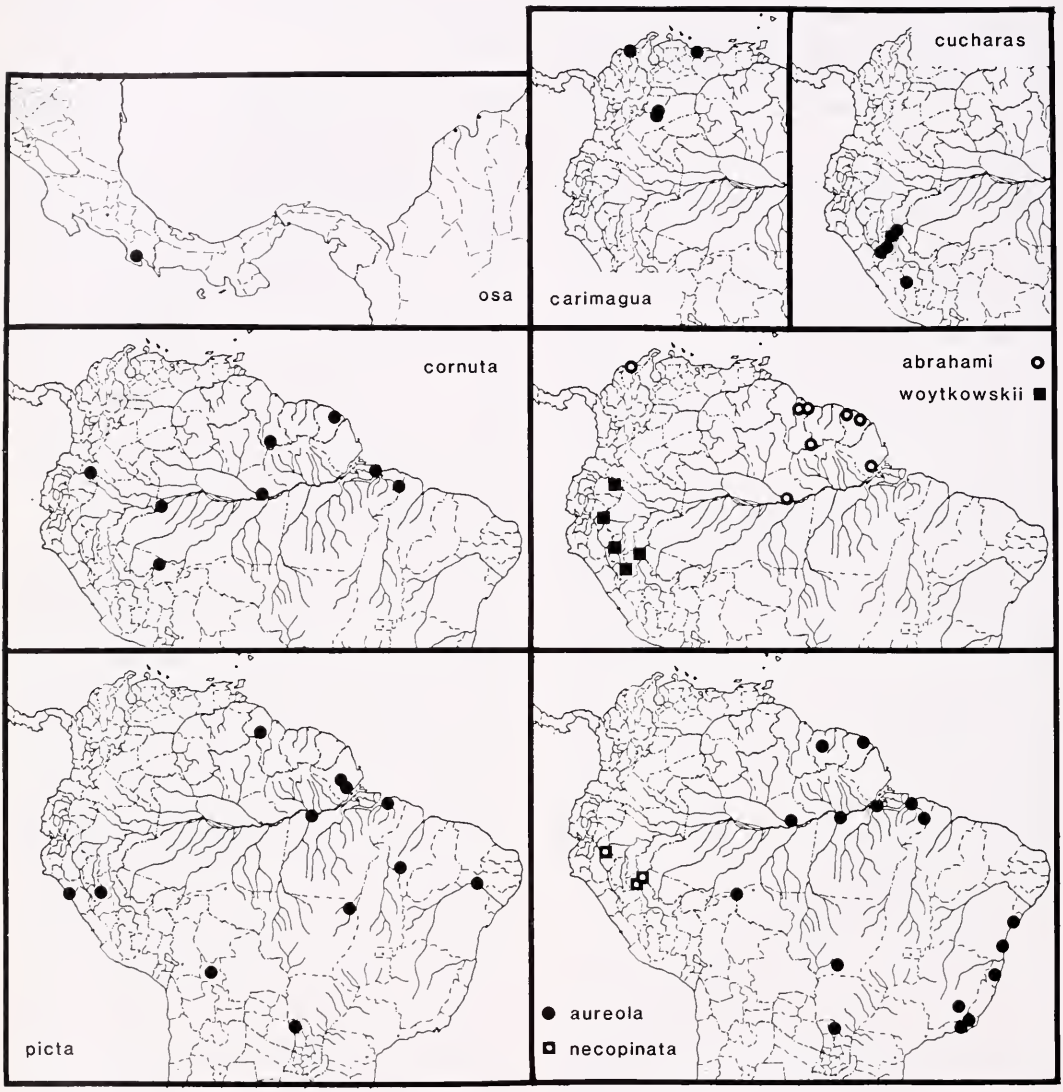
Misplaced. Chaetacis rouxi Mello-Leitão, 1939 is *Micrathena quadriserrata* F. P.-Cambridge. *Plectana incisa* Walckenaer, 1841 is not recognizable except that it is not a *Chaetacis*.

KEY TO *CHAETACIS*

Females

1. Abdomen with 12 spines (Figs. 792, 798, 804, 812, 837) 4
– Abdomen with (13 or) 14 spines (Figs. 827, 828, 844, 845, 853, 854) 2

2(1) Carapace with pair of spines on head (Fig.



Map 15. Distribution of *Chaetacis* species.

853); abdomen longer than wide (Fig. 854), with 14 spines and a tubercle on each side between anterior two pairs of spines (Fig. 854) ..... *necopinata*

– Carapace with pair of swellings on head (Figs. 827, 844); abdomen about as long as wide, without anterior lateral tubercles (Figs. 828, 845); Guyana to Brazil 3

3(2) Epigynum in profile with anterior and posterior slope of cone forming an acute angle (Fig. 849) ..... *aureola*

– Epigynum cone flat in profile (Fig. 832) ..... *abrahami*

4(1) Carapace with pair of spines on head (Figs. 803, 821) 5

– Carapace with pair of swellings on head (which may have more than one denticle; Figs. 792, 798, 837) 6

5(4) Abdomen square; fourth abdominal pair of spines larger than second (Figs. 803, 804); epigynum truncate in profile (Fig. 808); Guyana, Brazil to Colombia ..... *cornuta*

- Abdomen longer than wide; fourth abdominal pair of spines subequal to second (Fig. 822); epigynum pointed in profile (Fig. 826); Peru ..... *woytkowskii*

6(4) Abdomen trapezoidal, narrower in front than behind (Fig. 793); epigynum with notch in profile (Fig. 797); Costa Rica ..... *osa*

- Abdomen with sides parallel (Figs. 799, 813, 838); epigynum otherwise (Figs. 802, 817); South America 7

7(6) Epigynum truncate in profile (Fig. 802); Colombia, Venezuela ..... *carimagua*

- Epigynum pointed in profile (Figs. 817, 843) 8

8(7) Epigynum with blunt point in profile; anterior and posterior surface meet at about 45° (Fig. 817); Peru ..... *cucharas*

- Epigynum with acute point in profile (Fig. 843); Brazil to Paraguay ..... *picta*

Males

The males of *osa, carimagua, woytkowskii, abrahami* are not known.

1. Abdomen without prominent spines (Figs. 833, 850) 2

- Abdomen with spines (Figs. 809, 818, 859) 3

2(1) First tibia with proximal and distal end of equal width (Fig. 850); Guyana to Rio de Janeiro ..... *aureola*

- Proximal end of first tibia swollen, bearing spines pointing at distal end (Fig. 833); Peru, Brazil to Paraguay ..... *picta*

3(1) Abdomen with 14 spines and a pair of humps between first and second pairs of spines (Fig. 859); Amazon ..... *necopinata*

- Abdomen with 12 spines or less 4

4(3) Paracymbium with a hook at one end (Fig. 811); mesal side of palpus with a small hook on median apophysis (Fig. 810); Colombia, Guyanas to Brazil ..... *cornuta*

- Paracymbium only slightly curved (Fig. 820); mesal side of palpus without small hook on median apophysis (Fig. 819); Peru ..... *cucharas*

Chaetacis osa new species
Figures 792–797; Map 15

Holotype. Female and broken female paratype from Rincón de Oro, Puntarenas Prov., Costa Rica (C. E. Valerio, MZCR). The specific name is a noun in apposition after the Osa Peninsula.

Description. Female. Carapace, sternum dark brown; carapace rim and anterior spines white. Legs brown. Dorsum of abdomen white with black patches; large spines brown; sides brown; venter brown with median and paired white patches. Sclerotized areas dark brown. Carapace with anterior double denticles on swelling, three pairs of deep dimples, a deep thoracic depression and small denticles posteriorly (Figs. 792, 793). Abdomen trapezoidal, widest behind, with small white spines on anterior margin and three pairs of large spines with a small pair below, posteriorly (Figs. 792, 793). A tiny white spine on dorsal surface at base of posterolateral spine. Total length, 4.2 mm. Carapace, 1.6 mm long, 1.2 mm wide. First femur, 1.2 mm; patella and tibia, 1.3 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm. Second patella and tibia, 1.2 mm; third, 0.7 mm. Fourth femur, 1.5 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm.

Diagnosis. Chaetacis osa differs from others by its distinctive epigynum (Figs. 795, 796) with a notch in profile (Fig. 797) and by the trapezoidal abdomen, widest behind (Fig. 793).

Chaetacis carimagua new species
Figures 798–802; Map 15

Holotype. Female from Carimagua, 100 m el., Dept. Meta, Colombia, October 1973 (W. Eberhard, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace brown, swellings on each side of head lighter, rim white. Sternum dark brown, coxae light, distal articles of legs brown. Dorsum of abdomen black and white; venter blackish with a white spot on each side. Sclerotized spots brown. Carapace with two tubercular swellings on head, three pairs of dimples and distinct thoracic depression and rim (Figs. 798, 799). Eyes subequal in size. Abdomen squarish with twelve spines (Fig. 799). Total length, 4.4 mm. Carapace, 1.7 mm long, 1.2 mm wide. First femur, 1.4 mm; patella and tibia, 1.4 mm; metatarsus, 1.0 mm; tarsus, 0.4 mm. Second patella and tibia, 1.2 mm; third, 0.9 mm. Fourth femur, 1.8 mm; patella and tibia, 1.4 mm; metatarsus, 1.1 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 4.2 to 4.7 mm.

Diagnosis. The epigynum of this species has a transverse keel on the bulge and a round median plate behind (Figs. 801, 802), unlike *C. picta.*

Distribution. Venezuela, Colombia (Map 15).

Paratypes. COLOMBIA: *Dept. Meta.* Carimagua, Oct. 1973, ♀ (W. Eberhard, MCZ); 20 km N Río Muco, 20 km S El Porvenir, Finca Chenevo, 170 m, ♀ (W. Eberhard, MCZ). *Magdalena.* Río Frío, 15 Oct. 1927, ♀ (G. Salt, MCZ). VENEZUELA: *Est. Carabobo.* Maracay, 1935, ♀ (P. C. Vogt, MCZ).

Chaetacis cornuta (Taczanowski)
Figures 803–811; Map 15

Acrosoma cornuta Taczanowski, 1873: 268, pl. 5, fig. 22, ♀. Female holotype from Cayenne, French Guiana (PAN), examined.

Chaetacis cornuta:—Roewer, 1942: 952. Bonnet, 1956: 1031.

Description. Female. Carapace with large spine behind eyes (Figs. 803, 804). Abdomen with six pairs of spines, three pairs dorsal, the second and fourth large and black (Figs. 803, 804). Total length, 4.0 mm. Carapace, 1.7 mm long, 1.3 mm wide. First femur, 1.3 mm; patella and tibia, 1.4 mm; metatarsus, 0.9 mm; tarsus, 0.7 mm. Second patella and tibia, 1.2 mm; third, 0.8 mm. Fourth femur, 1.6 mm; patella and tibia, 1.4 mm; metatarsus, 1.0 mm; tarsus, 0.7 mm.

Male. Carapace with three pairs of dimples and circular thoracic mark; margin serrated. Side of head with swelling (Fig. 809). Abdomen with six pairs of spines (Fig. 809). Total length, 2.9 mm. Carapace, 1.2 mm long, 1.0 mm wide. First femur, 1.1 mm; patella and tibia, 1.2 mm; metatarsus, 0.8 mm; tarsus, 0.4 mm. Second patella and tibia, 1.1 mm; third, 0.6 mm. Fourth femur, 1.2 mm; patella and tibia, 0.9 mm; metatarsus, 0.7 mm; tarsus, 0.4 mm.

Variation. Females vary from 4.3 to 5.1 mm in total length, males from 2.9 to 3.0 mm. The cone of the epigynum of Colombian specimens is longer than that of specimens from Brazil. The female from Alto Solimões had the abdomen longer than wide.

Note. Males have been collected twice with females in Colombia. Figures 803, 804, 806–808 were made from the holotype of *C. cornuta.*

Diagnosis. Females differ from most other species by having a spine on each side of the head and by having only twelve spines on the abdomen (Figs. 803, 804). It differs from *M. woytkowskii* by having the abdomen squarish and the truncate eqigynum (Figs. 804, 808). The paracymbium of the male has a diagnostic hook (Fig. 811).

Distribution. Guianas, Amazon area (Map 15).

Records. COLOMBIA: *Putumayo.* near Puerto Asis, 4♀, ♂ (W. Eberhard MCZ); Buena Vista, 3♀, 2♂ (W. Eberhard, MCZ). GUYANA: 1913, ♀ (Parrish, CUC); Kuyuwini Riv., Essequibo Riv., 22 Nov. 1937, Dec. 1937, ♀ (W. G. Hassler, AMNH). BRAZIL: *Est. Pará.* 12 km W of Canindé, Rio Gurupi, April 1963, 3♀ (B. Malkin,

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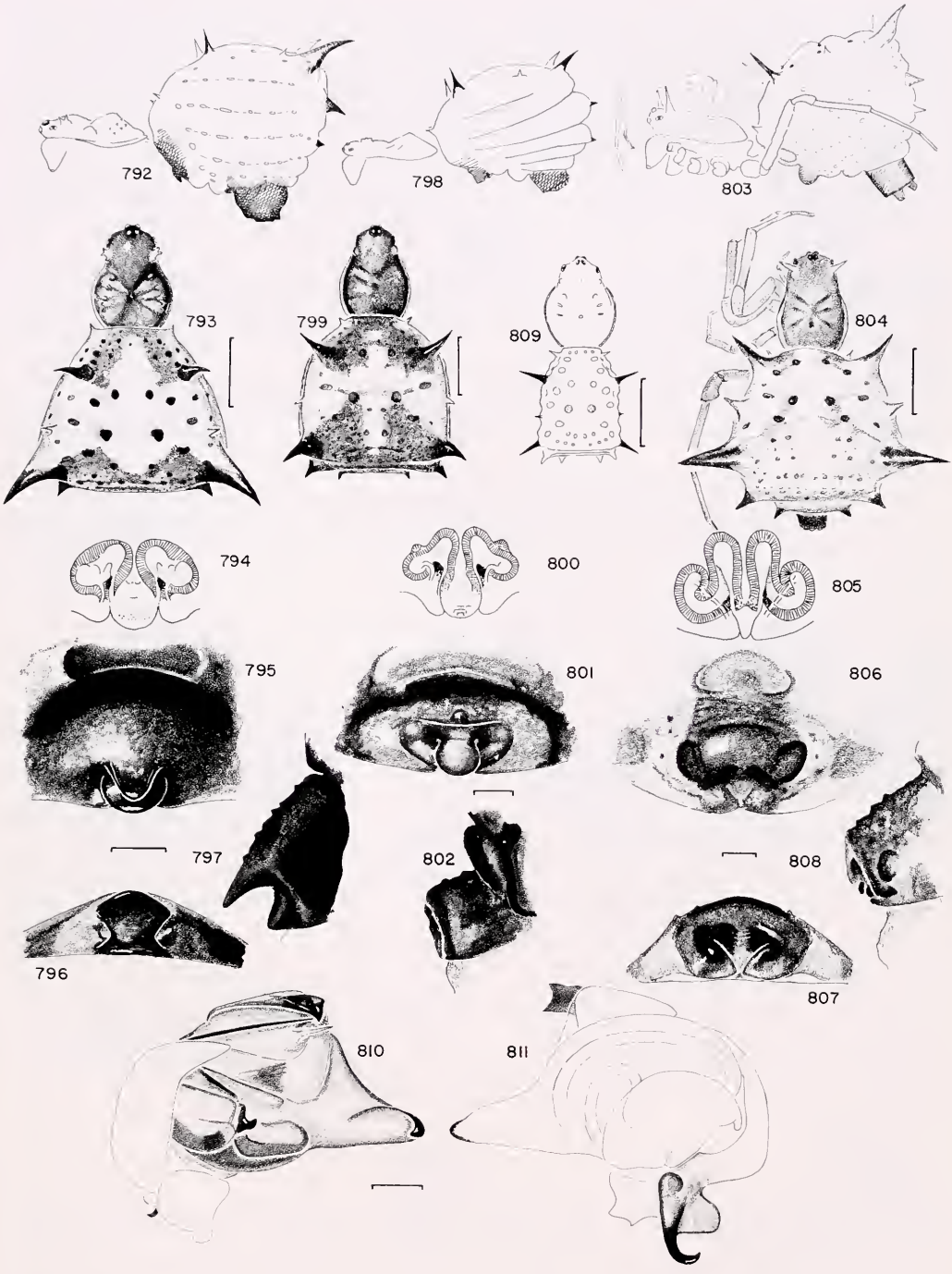
Figures 792–797. *Chaetacis osa* n. sp., female. 792. Lateral. 793. Dorsal. 794–797. Epigynum. 794. Dorsal, cleared. 795. Ventral. 796. Posterior. 797. Lateral.

Figures 798–802. *Chaetacis carimagua* n. sp., female. 798. Lateral. 799. Dorsal. 800–802. Epigynum. 800. Dorsal, cleared. 801. Ventral. 802. Lateral.

Figures 803–811. *Chaetacis cornuta* (Taczanowski). 803–808. Female. 803. Lateral. 804. Dorsal. 805–808. Epigynum. 805. Dorsal, cleared. 806. Ventral. 807. Posterior. 808. Lateral. 809–811. Male. 809. Dorsal. 810. Left palpus, mesal. 811. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 792, 793, 798, 799, 803, 804, 809, 1.0 mm.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AMNH); Canindé, June 1963, ♀ (B. Malkin, AMNH), 1964, 6♀ (J. Carvalho, AMNH); Cachoeira, Nov. 1952, ♀ (A. R. Hoge, IBSP). *Amazonas.* Manaus, Aug. 1971, ♀ (M. E. Galiano, MEG); Alto Solimões, Dec. 1979, ♀ (A. Lise, FZRS). *Acré.* Rio Alto Purus, W of Sena Madureira, 8 Nov. 1973, ♀ (B. Patterson, MCZ).

Chaetacis cucharas new species
Figures 812–820; Map 15

Holotype. Female with male paratype from Cucharas, Huallaga Valley, Dept. Huánuco, Peru, April 1954 (F. Woytkowski) in the Museum of Comparative Zoology. The specific name is a noun in apposition after the type locality.

Description. Female. Carapace brown with head swellings and rim lighter. Sternum dark brown, legs brown. Dorsum of abdomen dark brown with white patches; sides, venter brown. Carapace with three pairs of deep grooves, rim, thoracic depression; swellings on each side of head have denticles (Fig. 812). Abdomen square with fairly long spines (Figs. 812, 813). Total length, 5.0 mm. Carapace, 1.8 mm long, 1.3 mm wide. First femur, 1.3 mm; patella and tibia, 1.6 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm. Second patella and tibia, 1.4 mm; third, 0.9 mm. Fourth femur, 1.9 mm; patella and tibia, 1.6 mm; metatarsus, 1.2 mm; tarsus, 0.5 mm.

Male. Orange except for black abdomen spines and black book-lungs. Carapace with three pairs of dimples, circular thoracic depression and teeth around thoracic margin. Scattered small blunt teeth on head and carapace (Fig. 818). First tibia slightly S-shaped. Abdomen longer than wide, with twelve spines (Fig. 818). Total length, 3.0 mm. Carapace, 1.3 mm long, 1.0 mm wide. First femur, 1.0 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm. Second patella and tibia, 1.1 mm; third, 0.6 mm. Fourth femur, 1.1 mm; patella and tibia, 1.0 mm; metatarsus, 0.8 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 4.2 to 5.2 mm, males from 2.6 to 3.2 mm.

Note. Males and females have been collected together several times, but one male was collected with *C. woytkowskii* at Las Palmas, Peru.

Diagnosis. The bulge of the female eqigynum is lower than that of *C. picta* (Figs. 815–817) and, unlike other species, the inner and outer parts of the seminal recepticles are of equal length (Fig. 814). The male differs from others by the tubular shape of the paracymbium (Fig. 820) and the triangular shape of the conductor (Fig. 819).

Distribution. Peru (Map 15).

Paratypes. PERU: *Dept. Ucayali.* Colonia Calleria, 15 km from Ucayali, 1–16 Oct. 1961, 5♀, 2♂ (B. Malkin, AMNH); Pucallpa, Nov. 1946, ♀ (J. C. Pallister, AMNH). *Huánuco.* Cucharas, Huallaga Valley, Feb.–April 1954, 2♀, 2♂ (F. Woytkowski, EPC); Tingo María, 2 June 1967, ♀ (A. F. Archer, AMNH), Oct. 1946, ♀, 21 Nov. 1946, 2♀, 28 May 1947, ♀ (J. C. Pallister, AMNH); Yurac, 107 km E of Tingo María, 16 Nov. 1954, ♀ (E. I. Schlinger, E. S. Ross, CAS); Monsón Valley, Tingo María. 1954, numerous coll. of ♀♀, ♂♂ (E. I. Schlinger, E. S. Ross, CAS); 8 km W Las Palmas, 5 Oct. 1954, ♂ (E. I. Schlinger, E. S. Ross, CAS). *Ayacucho.* Monterico, ♂ (D. Jelski, PAN).

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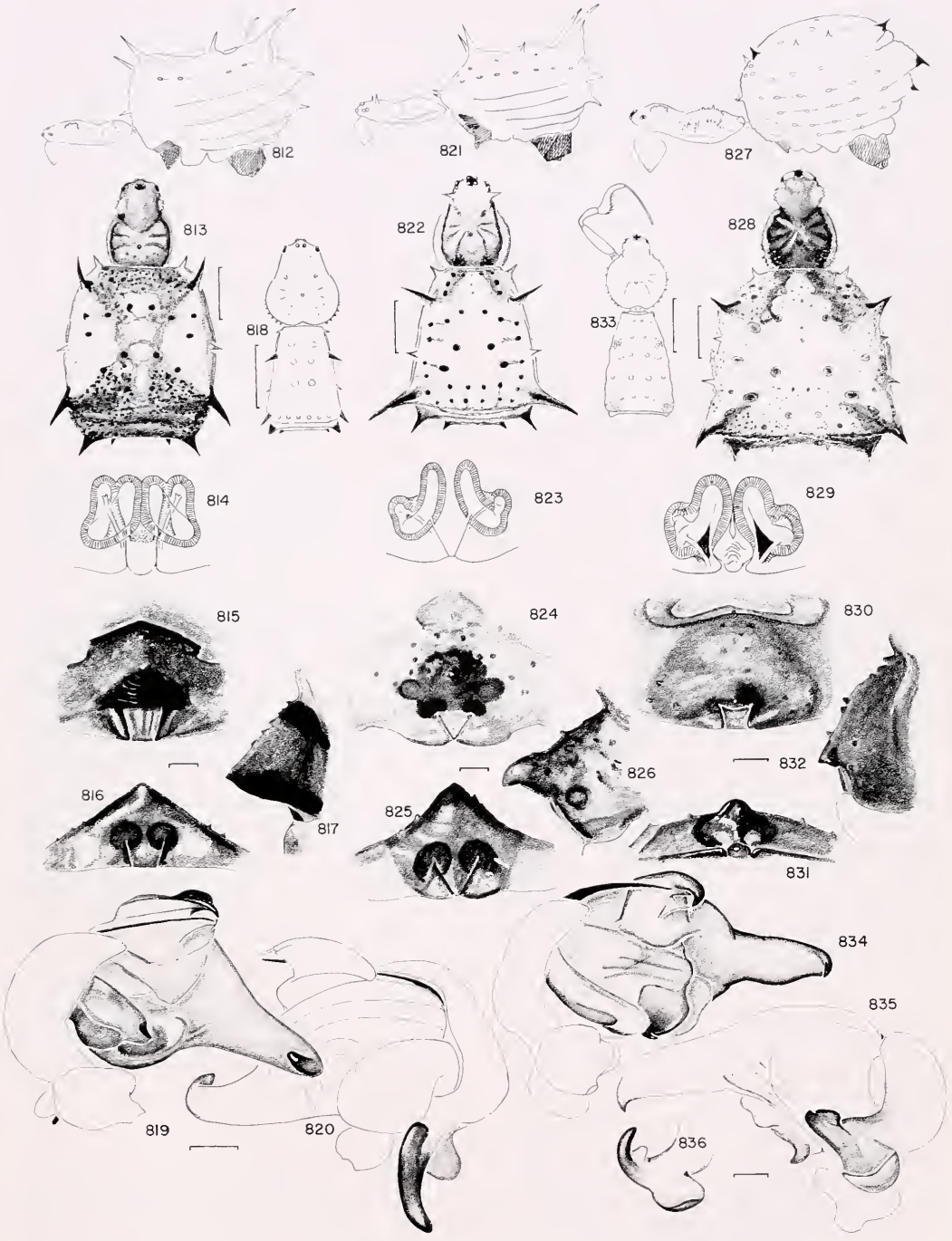
Figures 812–820. *Chaetacis cucharas* n. sp. 812–817. Female. 812. Lateral. 813. Dorsal. 814–817. Epigynum. 814. Dorsal, cleared. 815. Ventral. 816. Posterior. 817. Lateral. 818–820. Male. 818. Dorsal. 819. Left palpus, mesal. 820. Palpus, lateral.

Figures 821–826. *Chaetacis woytkowskii* n. sp., female. 821. Lateral. 822. Dorsal. 823–826. Epigynum. 823. Dorsal, cleared. 824. Ventral. 825. Posterior. 826. Lateral.

Figures 827–832. *Chaetacis abrahami* Mello-Leitão, female. 827. Lateral. 828. Dorsal. 829–832. Epigynum. 829. Dorsal, cleared. 830. Ventral. 831. Posterior. 832. Lateral.



Figures 833–836. *Chaetacis picta* (C. L. Koch), male. 833. Dorsal. 834. Palpus, mesal. 835. Palpus, lateral. 836. Paracymbium, lateral (Peru).

Scale line. 0.1 mm, except Figures 812, 813, 818, 821, 822, 827, 828, 833, 1.0 mm.

Chaetacis woytkowskii new species
Figures 821–826; Map 15

Holotype. Female and ten female paratypes from Cucharas, Huallaga Valley, Dept. Huánuco, Peru, Feb.–April 1954 (F. Woytkowski, MCZ). The species is named after the collector.

Description. Female. Carapace orange, black posteriorly. Sternum, legs orange. Dorsum of abdomen white except for large black spines; sides, venter orange; heavily sclerotized areas black. Carapace with two spines on head, three pairs of dimples in grooves, distinct thoracic depression and a very wide rim (Figs. 821, 822). Abdomen with twelve spines; longer than wide, widest posteriorly (Figs. 821, 822). Total length, 4.8 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 1.6 mm; patella and tibia, 1.6 mm; metatarsus, 1.1 mm; tarsus, 0.5 mm. Second patella and tibia, 1.3 mm; third, 0.9 mm. Fourth femur, 1.8 mm; patella and tibia, 1.5 mm; metatarsus, 1.2 mm; tarsus, 0.5 mm.

Variation. Females vary in total length from 4.5 to 5.0 mm.

Note. A male collected with females at Las Palmas, Peru appeared to be *M. cucharas*, and was placed with that species.

Diagnosis. Chaetacis woytkowskii differs from *C. cornuta* by having a longer abdomen, the second and fourth spines subequal in size (Figs. 821, 822), and by having the epigynum more cone-shaped in profile (Figs. 825, 826); it differs from *M. cucharas* by having spines rather than tubercles behind the eyes (Figs. 821, 822).

Distribution. Ecuador, Peru (Map 15).

Paratypes. ECUADOR: *Prov. Napo.* R. F. Cuyabeno, 14 Feb. 1984, ♀ (L. Avilés, MECN). PERU: *Dept. Huánuco.* Cucharas, Huallaga Valley, Feb.–April 1954, 47♀ (F. Woytkowski, EPC); Santa Teresa, Huallaga Valley, Aug. 1954, 6♀ (F. Woytkowski, EPC); Tingo María, Monsón Valley, 26 Oct. 1954, ♀, 19 Oct. 1954, ♀, 28 Oct. 1954, 2♀ (E. I. Schlinger, E. S. Ross, CAS), 8 Oct. 1948, ♀, 26 May 1947, ♀ (J. C. Pallister, AMNH), 5 June 1967, 2♀ (A. F. Archer, AMNH), Oct. 1946, ♀ (W. Weyrauch, EPC); 8 km W Las Palmas, 5 Oct. 1954, ♀ (E. I. Schlinger, E. S. Ross, CAS). *San Martín.* Bellavista, 11 Dec. 1946, ♀, ♂ (J. C. Pallister, AMNH). *Amazonas.* Río Alto Marañón betw. Río Campa and Río Nieva, 10–24 Sept. 1924, ♀ (Klug, AMNH). *Ucayali.* Río Calleria, 15 km from Ucayali, Oct. 1961, 3♀ (B. Malkin, AMNH).

Chaetacis abrahami Mello-Leitão
Figures 827–832; Map 15

Chaetacis abrahami Mello-Leitão, 1948: 162. Female holotype from Yawakuri River, Guyana, July 1919 (BMNH), examined.

Chaetacis minima Mello-Leitão, 1948: 163. Immature male and immature female syntypes from Kuruabaru Creek, Guyana, Sept. 1919 (BMNH), examined. NEW SYNONYMY.

Chaetacis tuberculata Chickering, 1959: 472, figs. 20–24, ♀. Female holotype and one paratype from source of Kutari River, British Guyana (BMNH), examined. NEW SYNONYMY.

Synonymy. The type vial of *C. abrahami* is labeled "manuscript name" in Chickering's handwriting. The species description has been missed by the Zoological Record, and Chickering apparently overlooked it. It is recorded in the Brignoli (1983) catalog. *C. minima* are immatures with the full number of spines.

Description. Female. Carapace with head swellings bearing denticles (Fig. 828); thoracic region with a median depression and four deep grooves dividing swellings bearing teeth. Abdomen squarish with seven pairs of spines. Total length, 5.2 mm. Carapace, 2.0 mm long, 1.4 mm wide. First femur, 1.5 mm; patella and tibia, 1.6 mm; metatarsus, 1.0 mm; tarsus, 0.5 mm. Second patella and tibia, 1.3 mm; third, 0.9 mm. Fourth femur, 1.9 mm; patella and tibia, 1.4 mm; metatarsus, 1.2 mm; tarsus, 0.5 mm.

Variation. Females varied from 4.5 to 5.2 mm.

Note. The male is unknown; a male of *Micrathena pungens* has been collected with this species in Manaus.

Diagnosis. This species differs from *C. aureola* and other 14-spined species by the relatively flat epigynum (Figs. 830–832).

Distribution. Colombia, Guyana to Mato Grosso, Brazil (Map 15).

Records. GUYANA: Canje, Ikuruwa River, 1961, ♀ (G. Bentley, AMNH). FRENCH GUIANA: Cayenne, ♀ (K. Jelski, PAN); St. Laurent de Maroni, 6♀ (K. Jelski, PAN). COLOMBIA: *Dept. Magdalena.* Río Frío, 25 July 1926, ♀ (F. W. Walker, AMNH). BRAZIL: *Terr. Amapá.* Villa Amazonas, 29 May 1964, 8♀ (C. E., E. S. Ross, CAS). *Est Amazonas.* Manaus, Aug. 1971, 3♀ (M. E. Galiano, MEG). *Mato Grosso.* Oct. 1976, ♀ (M. Alvarenga, AMNH).

Chaetacis picta (C. L. Koch)
Figures 833–843; Map 15

Acrosoma pictum C. L. Koch, 1836: 61, pl. 214, ♀. Female from Brazil (ZSM), destroyed.

Micrathena conspicua Mello-Leitão, 1929: 110, pl. 21, ♀. Female holotype from Tapera, Pernambuco, in vial labeled *M. tigris* (MNRJ), examined; 1932, fig. 3, ♀. NEW SYNONYMY.

Chaetacis evansi Chickering, 1959: 469, figs. 12–16, ♂. Male holotype from Monte Allegro Forest, Santarém, Brazil (BMNH), examined. NEW SYNONYMY.

Chaetacis rugosa Chickering, 1959: 471, figs. 17–19, ♀. Female holotype, four female paratypes from Monte Allegro Forest, Santarém, Brazil (BMNH), examined. NEW SYNONYMY.

Synonymy. Koch's illustration for a twelve-spined *Chaetacis* fits this species best, particularly the color markings. Chickering named the male *evansi*, the female *rugosa*.

Description. Female. Thorax with four pairs of dark grooves; tiny spines between third and fourth grooves (Figs. 837, 838). Abdomen squarish with six pairs of spines and many small sclerotized disks (Figs. 837, 838). Total length, 5.4 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 1.4 mm; patella and tibia, 1.5 mm; metatarsus, 1.1 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.9 mm. Fourth femur, 1.9 mm; patella and tibia, 1.4 mm; metatarsus, 1.1 mm; tarsus, 0.5 mm.

Male holotype of *evansi*. Carapace with small teeth around edge, two small areas bearing teeth on head, one on each side, and three pairs of swollen areas on carapace (Fig. 833). Abdomen without spines, longer than wide, narrower anteriorly than posteriorly, with folds on posterior and anterolateral edges. First leg with tibia swollen at proximal end, distal end strongly curved (Fig. 833). Total length, 3.4 mm. Carapace, 1.6 mm long, 1.1 mm wide. First femur, 1.0 mm; patella and tibia, 1.2 mm; metatarsus, 0.8 mm; tarsus, 0.4 mm. Second patella and tibia, 1.2 mm; third, 0.6 mm. Fourth femur, 1.4 mm; patella and tibia, 1.0 mm; metatarsus, 0.7 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 4.0 to 5.6 mm. Females from Mato Grosso may have the tubercular swellings in the head region cone-shaped. They perhaps belong to a different species.

Note. The only male collected with a female came from Santana, Rio Matapí. It is uncertain whether they belong together. However, both female and male resemble the 14-spined *C. aureola*. The illustrations (Figs. 837–841) were made from the type of *C. rugosa*; those of the male (Figs. 833–835) from *C. evansi*. The male appears to have its paracymbium broken. The paracymbium of the male from Peru is also illustrated (Fig. 836).

Diagnosis. The female can be separated from other 12-spined species by the longer cone-shaped bulge of the epigynum (Figs. 841-843). The male can be distinguished by the shape of the paracymbium and the swollen first tibia (Figs. 833, 835, 836). The species is probably close to *C. aureola*.

Range. Guyana to Paraguay (Map 15).

Records. GUYANA: *Kartabo.* 1924, ♀ (CUC). PERU: *Dept. Huánuco.* Monsón Valley, Tingo María, 12 Oct. 1942, ♂ (E. I. Schlinger, E. S. Ross, CAS). BRAZIL: *Terr. Amapá.* Santana, Rio Matapí, June 1966, 2♀, ♂, imm. (M. E. Galiano, MEG); Serra do Navio, June 1966, 2♀ (M. E. Galiano, MEG). *Est. Pará.* Val-de-Cans, Belém, 20–21 Nov. 1963, ♀ (Oliveira, P. Wygodzinsky, AMNH). *Maranhão.* Santa Barbara, São Felix de Balsas, May–June 1965, 2♀ (G. Eiten, AMNH). *Mato Grosso.*

Jaciara, June 1963, ♀ (M. Alvarenga, AMNH); Barra do Tapirapé, Nov. 1960, 2♀, Dec. 1961, ♀ (B. Malkin, AMNH). BOLIVIA: *Dept. Cochabamba*. Feb. 1952, ♀ (Martina, MULP). PARAGUAY: San Luiz [?], Oct. 1908, ♀ (AMNH).

Chaetacis aureola (C. L. Koch)
Figures 844–852; Map 15

Acrosoma aureolum C. L. Koch, 1836: 60, fig. 213, ♀. Female from Brazil (ZSM), destroyed.

Acrosoma affinis C. L. Koch, 1839: 131, fig. 525, ♀. Female from Brazil (ZSM), destroyed. NEW SYNONYMY.

Chaetacis affinis:—Simon, 1895: 863. Roewer, 1942: 951. Bonnet, 1956: 1030.

Chaetacis hirsuta Mello-Leitão, 1932:96, fig. 7, ♀. Female holotype from Pará [Belém], Brazil (MNRJ), examined. NEW SYNONYMY.

Chaetacis aculeata Chickering, 1959: 466, figs. 1–5, ♀. Female holotype from Gurupá, Brazil (BMNH), examined. NEW SYNONYMY.

Chaetacis dentata Chickering, 1959: 468, figs. 6–11, ♂. Male holotype from Gurupá, Brazil (BMNH), examined. NEW SYNONYMY.

Synonymy. The description of *A. aureolum* fits this species, although C. L. Koch does not mention or show the head swellings. They are at times quite indistinct. Koch later gave a description of the diagnostic head swellings and the spination for *A. affinis*, leaving no doubt as to its identity. Chickering named the female *aculeata*, the male *dentata*.

Description. Female. Carapace with spiny swellings on each side of head; dimples on each side of thorax in deep grooves; bulges between grooves with denticles. Abdomen almost square in dorsal view, with seven spines on each side, the second and fifth the largest, and many sclerotized discs, both large and minute (Figs. 844, 845). Total length, 5.0 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 1.5 mm; patella and tibia, 1.6 mm; metatarsus, 1.0 mm; tarsus, 0.5 mm. Second patella and tibia, 1.4 mm; third, 0.9 mm. Fourth femur, 1.9 mm; patella and tibia, 1.4 mm; metatarsus, 1.2 mm; tarsus, 0.5 mm.

Male. Carapace like female. Patella of first leg with a small lobe on outside, bearing a macroseta. Tibia of first leg very curved and with macrosetae on underside. Abdomen trapezoidal, without spines (Fig. 850). Total length, 3.0 mm. Carapace, 1.4 mm long, 1.0 mm wide. First femur 0.9 mm; patella and tibia, 0.9 mm; metatarsus, 0.6 mm; tarsus, 0.4 mm. Second patella and tibia, 1.0 mm; third, 0.6 mm. Fourth femur, 1.2 mm; patella and tibia, 0.9 mm; metatarsus, 0.6 mm; tarsus, 0.4 mm.

Variation. Females vary 4.5 to 5.2 mm total length, males 3.0 to 3.8 mm. Many females have a longer, larger swelling with denticles on each side of the head. But the size of these denticles is variable. Several females from Rio de Janeiro have 13 spines on the abdomen, missing a small one on one side. The shape of the epigynal cone is variable. The paracymbium is longer in the palpus of a male from Rio de Janeiro.

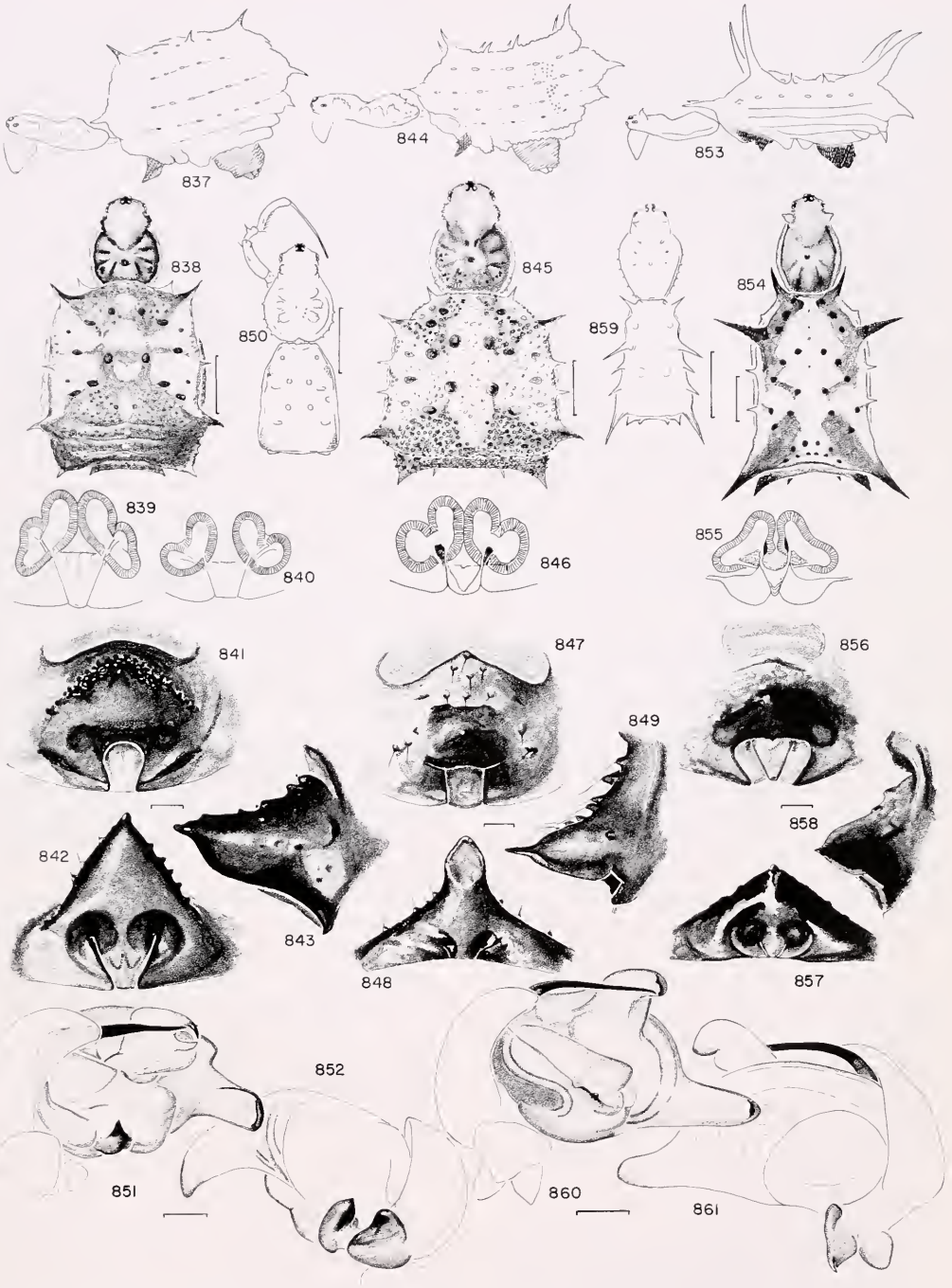
Note. Males are commonly collected with females. Penultimate females have the same number of abdominal spines on the abdomen as adult females. Figures 844–849 were made from paratypes of *C. aculeata*; Figures 850–852 from the holotype of *C. dentata*.

Diagnosis. Females differ from *C. picta* by having 14 rather than 12 spines (Figs. 844, 845); males by the differently shaped paracymbium (Fig. 852). Females of *C. aureola* differ from *C. abrahami* by hav-

→

Figures 837–843. *Chaetacis picta* (C. L. Koch), female. 837. Lateral. 838. Dorsal. 839–843. Epigynum. 839, 840. Dorsal, cleared. 841. Ventral. 842. Posterior. 843. Lateral. 839. (Belém, Brazil). 840. (Barra da Tapirapé, Brazil). 841–843. (Santarém, Brazil).

Figures 844–852. *Chaetacis aureola* (C. L. Koch). 844–849. Female. 844. Lateral. 845. Dorsal. 846–849. Epigynum. 846. Dorsal, cleared. 847. Ventral. 848. Posterior. 849. Lateral. 850–852. Male. 850. Dorsal. 851. Left palpus, mesal. 852. Palpus, lateral.



Figures 853–861. *Chaetacis necopinata* (Chickering). 853–858. Female. 853. Lateral. 854. Dorsal. 855–858. Epigynum. 855. Dorsal, cleared. 856. Ventral. 857. Posterior. 858. Lateral. 859–861. Male. 859. Dorsal. 860. Palpus, mesal. 861. Palpus, lateral.

Scale lines. 0.1 mm, except Figures 837, 838, 844, 845, 850, 853, 854, 859, 1.0 mm.

ing a cone-shaped epigynum (Figs. 847–849).

Natural History. Specimens have been collected by D. Smith in Suriname in swamp forest with the web center 1 m above the ground, and in mountain savannah forest, 45 cm above the ground.

Distribution. Suriname to southeastern Brazil (Map 15).

Records. SURINAME: *Saramacca Prov.* Voltzberg-Raleighvallen Nature Reserve, Feb. 1982, 5♀, ♂ (D. Smith Trail, MCZ). FRENCH GUIANA: Cayenne, ♀ (K. Jelski, PAN). BRAZIL: *Est. Pará.* Santarém, forest, 1896, 3♀ (F. O. P.-Cambridge, E. E. Austin, BMNH); Belém, 12 Feb. 1959, ♀, ♂ (A. M. Nadler, AMNH), July 1971, ♀ (T. McGrath, MCZ); 50 km E of Canindé, Rio Gurupi, 22–25 Feb. 1966, ♀, ♂ (B. Malkin, AMNH). *Amazonas.* Manaus, Aug. 1971, ♀ (M. E. Galiano, MEG). *Rondônia.* Abunã, March 1922, ♀ (J. H. Williamson, MCZ). *Bahia.* Itamarajú, 7 Dec. 1978, ♀ (J. Santos, FZRS); Camacari, 2 Dec. 1977, ♂ (J. Santos, FZRS); Ilhéus, Jan. 1964, 2♀ (Papavero, FZRS), ♀ (MZSP). *Mato Grosso.* Chapada dos Guimarães, Nov. 1963, 2♀, ♂ (M. Alvarenga, AMNH). *Minas Gerais.* Ponte Nova, Rio Casca, Feb. 1953, ♀ (Schubart, MZSP). *Rio de Janeiro.* San Antonio do Imbé, Jan. 1961, 8♀, ♂ (M. Alvarenga, AMNH); Pinheiro, ♀ (MNRJ). PARAGUAY: *Dept. Amambay.* Cerro Corá, Oct. 1981, ♀ (J. Kochalka, JAK).

Chaetacis necopinata (Chickering) new combination
Figures 853–861; Map 15

Micrathena necopinata Chickering, 1960c: 84, figs. 71–73, ♂. Male holotype from the Amazon (HEO), examined.

Note. The exact type locality is unknown.

Description. Female. Carapace orange with white rim; black patch posteriorly on each side of thorax. Sternum dark brown. Coxae and femora orange, distal articles of legs brown. Dorsum of abdomen white with black patches; sides white and black; venter white and black with book-lungs black; ring around spinnerets black. Carapace with two semi-triangular spines on head, fairly smooth, with two pairs of dimples, a round thoracic depression and rim. Abdomen longer than wide, with 14 spines and pair of tubercles anterolaterally (Figs. 853, 854); dorsal white areas smooth; dark posterior and ventral areas punctate. Total length, 6.2 mm. Carapace, 2.3 mm long, 1.5 mm wide. First femur, 1.9 mm; patella and tibia, 1.9 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm. Second patella and tibia, 1.7 mm; third, 1.2 mm. Fourth femur, 2.4 mm; patella and tibia, 1.9 mm; metatarsus, 1.4 mm; tarsus, 0.6 mm.

Male. Carapace with pair of spines in head region, two pairs of indistinct dimples, distinct thoracic depression, and thoracic area rough. First leg not modified. Abdomen with 14 spines (Fig. 859). Total length, 3.4 mm. Carapace, 1.4 mm long, 0.9 mm wide. First femur, 1.2 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.4 mm. Second patella and tibia, 1.1 mm; third, 0.6 mm. Fourth femur, 1.3 mm; patella and tibia, 1.0 mm; metatarsus, 0.8 mm; tarsus, 0.4 mm.

Variation. Females vary in total length from 4.9 to 6.1 mm.

Note. The spination of the abdomen and the head spine suggest that the female belongs with the male of *C. necopinata.*

Diagnosis. This is the only species having 14 abdominal spines and a pair of spines (rather than swellings) on the head (Figs. 853, 854). The male differs from all others by having a pair of spines on the head and having 14 abdominal spines (Fig. 859).

Distribution. Northeastern Peru (Map 15).

Paratypes. PERU: *Dept. Amazonas.* Río Alto Marañón, betw. Río Campa and Río Nieva, Sept. 1924, ♀ (Klug, AMNH). *Ucayali.* Colonia Calleria, Río Calleria, 15 km from Ucayali, 10–30 Sept. 1961, ♀, 1–16 Oct. 1961, ♀ (B. Malkin, AMNH); Pu-

callpa, 2 Oct. 1954, ♀ (E. I. Schlinger, E. S. Ross, CAS).

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